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A review of the genus *Stenochlaena* (Blechnaceae, subfamily Stenochlaenoideae)

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Abstract

Stenochlaena is a small but widespread genus confined to the tropics and subtropics of the Old World. A key to the species, updated descriptions, distribution-maps, and detailed drawings are provided. Also included is a key to assist in separating several genera that are most often confused with *Stenochlaena*. There is morphological evidence suggesting that hybrids may exist between several species in Malesia. Although primarily a rainforest genus, the distribution patterns of the various species of *Stenochlaena* appear closely related to ecological requirements; the hemiepiphytic members of the genus are most frequently present along forest margins in relatively high light conditions with access to a moist soil or an aquatic environment but not necessarily to perpetually humid atmospheric conditions.

Introduction

Stenochlaena J.Sm. is a small genus of six (or possibly seven) species confined to the old-world tropics and sub-tropics. No species have been recorded from the Americas, including associated islands and the Caribbean; claims for the presence of *Stenochlaena* in these regions all appear to be based on earlier and broader generic concepts that included species of *Lomariopsis* Fée.

In the early literature there was much confusion over the generic limits of *Stenochlaena*, especially in relation to the genera *Lomariopsis* and *Teratophyllum* Mett. ex Kuhn. However, it was the contribution by Holttum (1932) that defined the currently accepted boundaries of the three genera. Holttum (1966) extended this work to include the definition of *Lomagramma* J.Sm. in his consideration of the Pacific and Malesian occurrences of *Lomariopsis* and *Teratophyllum*. Holttum added to his treatment of *Teratophyllum* in the *Flora of Malaysia* (1968) and the neotropical species of *Lomariopsis* have recently been revised and monographed by Moran (2000).

Holttum (1971) described an additional species, *Stenochlaena cumingii*, briefly summarising the information then available for the genus and providing a key to the species.

The present study on *Stenochlaena* is an extension and update largely based on additional collections considered together with those used in Holttum's pioneering studies of the genus.

In herbarium collections there continues to be confusion of members of the genus *Stenochlaena* (Blechnaceae) with genera in the family Lomariopsidaceae, *Lomagramma*, *Lomariopsis*, and *Teratophyllum*. All four genera are mostly hemiepiphytic occurring in rainforest habitats, with mature plants usually producing pinnate sterile fronds spaced along a climbing rhizome; most species have fertile laminae that are once pinnate and the fertile pinnae are exindusiate but otherwise appearing lomarioid in external morphology. The following key is provided to assist in distinguishing *Stenochlaena* from the above three genera of the Lomariopsidaceae.

Key

1a. Pinnae of adult fronds with a closed network of areolae that lack free veins in the islets; rhizomes with deciduous clathrate scales .... ***Lomagramma***

1b. Areolae, if present, give rise to the lateral veins; rhizome scales not clathrate 2

2a. Lateral veins of the sterile pinnae arising from a closely parallel series of areolae on both sides of the costa; rhizome anatomy radially symmetrical; spores with a very thin and closely appressed perispore .... ***Stenochlaena***

2b. Veins free with lateral veins of the sterile pinnae arising directly from the costa; areolae not present; rhizome anatomy dorsiventral; spores with a conspicuous perispore 3

3a. Rhizome of adult plant slender, cylindrical, sometimes spiny; pinnae including the terminal pinna articulated; juvenile fronds with the lamina variably but finely dissected, forming bathyphylls .... ***Teratophyllum***

3b. Rhizome of adult plant robust, flattened and conspicuously covered in scales especially at the apex but not bearing spines; lateral pinnae articulated on the rhachis, but terminal pinna not articulated; juvenile fronds with lamina simply pinnate, bathyphylls absent .... ***Lomariopsis***

Taxonomic position of *Stenochlaena*

Holttum (1932), having demonstrated that the anatomy of *Stenochlaena* is distinctive and emphasizing the significance of the absence of an indusium, suggested that this genus be placed with or near to the acrostichoid ferns, a view he maintained throughout later studies (Holttum 1949, 1966, 1971).

Copeland (1947) abandoned his earlier view that *Stenochlaena* be placed with the asplenioid ferns (Copeland 1905), and concluded from venation, spore morphology and other characters that it was more logically placed in the Blechnaceae. This view contrasts with that of Ching (1978) who placed *Stenochlaena* in a new family 'incertae sedis', the Stenochlaenaceae Ching, independent from the pteridioid and blechnoid ferns but, like Holttum, he favoured a position near the acrostichicoid genera.

Based on a detailed developmental study, Stokey & Atkinson (1952) reported that the gametophyte of *Stenochlaena*, especially in the early stages of development, is morphologically very similar to that of several species of *Blechnum* and very different from *Acrostichum*.

Pichi-Sermolli (1977) considered *Stenochlaena*, in some of its features, to be more closely related to *Blechnum* than to *Brainea* and he concluded that '*Stenochlaena* represents a phyletic line, probably rather old, independent from both those of *Blechnum* and *Brainea*, but derived from the same ancestral source.' The stomatal structure (Van Cotthem 1970), venation, and the existence of some climbing species in the genus *Blechnum* gives some support to placing *Stenochlaena* closer to the genus *Blechnum*.

The significance of the lack of an indusium in *Stenochlaena*, a character shared with the genus *Brainea* may have been overemphasized by both Holttum and Ching in their separating *Stenochlaena* from the blechnoid ferns. While the venation pattern in *Stenochlaena* is essentially blechnoid, the stand-alone characters in *Stenochlaena* (if placed in the Blechnaceae) include its rhizome with a complex polycyclic dictyostele, a very complex multi-stele arrangement in the stipe and rhachis, the nature of the rhizome scales, and the characteristic spore ornamentation with the very thin and closely adhering perispore. Additionally, for some species there is the presence of a gland (sometimes two glands) at the bases of the lateral pinnae. These various distinctive features appear to justify a separate monogeneric subfamily, the Stenochlaenoideae (Kramer et al., in Kramer & Green 1990; Roux 2001) within the Blechnaceae, a view supported in the present study.

Stevenson & Loconte (1996), in their study of ordinal and familial relationships of pteridophyte genera based on a cladistic analysis of 116 characters, concluded that the genera *Stenochlaena* and *Brainea* could be resolved as early branches of the Blechnaceae; *Stenochlaena* they interpreted as a sister group to *Pteridoblechnum*. Molecular work using *rbc*L (Hasebe et al. 1995) is also consistent with this view, with the genera of the Blechnaceae (*Blechnum*, *Doodia*, *Sadleria*, and *Stenochlaena*) forming a well-supported clade with *Stenochlaena* sister to the other genera.

Cranfill & Kato (2003) in a recent study of the woodwardioid ferns, *Woodwardia* Sm., *Anchista* C.Presl and *Lorinseria* C.Presl, based on 22 morphological characters and a range of molecular markers, (*rbc*L, *rps4*, and *rps4–trnS* spacer) have clearly demonstrated that both *Stenochlaena* and *Blechnum* are consistently sister to the woodwardioid genera, clearly within a monophyletic Blechnaceae. In a more recent study, Smith et al (2006), in considering a classification of extant ferns, conclude that the family Blechnaceae consists of nine genera (including *Stenochlaena*) that nest within *Blechnum* s.l., but that acceptance is dependent upon a recircumscription of *Blechnum* s.l. Schuettpelz & Pryer (2008) also conclude that *Blechnum* is not monophyletic and that it requires further research.

Morphology and Terminology

In most members of the genus, *Stenochlaena* the rhizome is scandent, usually round in cross-section, 1–2.5 cm diameter and very long, often reaching the crowns of tall rainforest trees, but it maintains a connection with the ground (the one exception is *Stenochlaena areolaris*, a plant that grows epiphytically in natural water tanks usually in the crowns of palms etc.). As the plant climbs over rocks and forest debris and sometimes spreads as a floating mat over water surfaces, it gives rise to a succession of spaced fronds. No members form a woody caudex or trunk and none produces a true radial crown of fronds. Holttum (1932) described and illustrated the internal anatomy of the rhizomes of two species, *S. palustris* and *S. laurifolia* C. Presl (now *S. cumingii*), demonstrating that the stele has radial symmetry with 3 or 4 large bundles surrounded by numerous smaller bundles in two approximately concentric circles. The rhizome is capable of giving rise to roots and fronds from all sides but in most specimens, roots emerge only from areas coming into contact with the substratum and fronds arise from the opposite side, resulting in a false dorsiventral external morphology. The apical region of the rhizome is covered by scales, most of which are shed as the rhizome grows. Scales vary from peltate to acuminate but mostly with a peltate attachment and often are closely appressed to the rhizome surface.

The stipe may possess hairs and scales when young, but is glabrous or almost so at maturity; is grooved on the adaxial face and possesses two lateral lines of spaced glands, which are more easily observed in fresh material. Sterile lamina once pinnate in all taxa; however most species may on rare occasions produce aberrant bipinnate fronds. *Stenochlaena tenuifolia* is the only species regularly producing bipinnate fertile fronds. Most species have both sterile and fertile pinnae that are very shortly stalked and more or less articulate to the rhachis, but these are variable features both within and between taxa. Most species have a gland on the acropetal margin at the base of the lateral pinnae (or most of the lateral pinnae); more rarely there is also a gland on the basal margin. These glands possibly only function in the young stages of a frond's development, and on the mature sterile frond are small, dry, brown structures. A more detailed description can be found in Troll (1932). One of the morphological characteristics of *Stenochlaena* is that the lateral veins of the pinnae arise from a series of areolae sometimes close to the *costa*; when very closely parallel to the costa they may prove difficult to detect. The lateral veins arising from the areolar vein are either single or once bifurcate (less commonly twice) and each terminates within the pinna margin. Fertile fronds have the same basic pattern but the areolar vein pattern tends to be more complex; fertile pinnae in all species are very much more slender than the pinnae of the sterile fronds and the sori are linear on either side of the costa; although there is no protective indusium, some taxa have a narrow region of sterile tissue between the sorus and the pinna margin. During the maturation of the sporangia, the margins of the pinnae reflex, resulting in the soral surface appearing to completely cover the abaxial face of the pinna and further enhancing the acrostichoid appearance.

Spores of *Stenochlaena* are pale yellow or yellow-brown to hyaline, ellipsoidal, and monolete; the exospore has coarse, prominent tubercles with varying arrangements for each of the taxa. The perispore is very thin, difficult to detect unless sectioned, relatively smooth, and closely envelops the exospore. The distinctive structure of the spores of three species, as seen by light microscopy, were described and illustrated by Holttum (1932). They appeared to lack a perispore. However from a survey using both whole spores observed by scanning electron microscopy, and some wall details in sectioned material viewed by transmission electron microscopy, Tryon & Lugardon (1990) illustrated images of several species of *Stenochlaena* which all appear to have a thin, closely enveloping perispore.

Stenochlaena J.Sm.

Stenochlaena J.Sm., J. Bot. (Hooker) 3: 401 (1841), 4: 149 (1842).

Type: *Stenochlaena scandens* J.Sm. (= *Polypodium palustre* Burm.f., 1768; *Stenochlaena palustris* (Burm.f.) Bedd., 1876). Lectotype technically designated by Pfeiffer, Nom. bot. 2:1274 (1874).

Etymology: the genus *Stenochlaena* from Greek 'stenos' = slender, presumably referring to the pinnae of the very large fronds and 'chlaina' = cloak or mantle, referring to the climbing plants together with their very large sterile fronds cloaking the trunk and canopy of a rainforest host tree.

Rhizome creeping and scandent, maintaining connection with the ground, hence hemiepiphytes except for a single species which is essentially a crown aquatic epiphyte with no direct connection with the soil; rhizome internal anatomy a complex perforated dictyostele with radial symmetry which in cross-section has a few large central steles and two more peripheral rings with numerous small vascular bundles; young rhizome green, with sparse small, usually appressed, brown peltate and/or linear-acuminate brown *scales*, sometimes clathrate and with fine marginal outgrowths; as rhizome matures most of the scales are shed leaving a few that are scattered and closely appressed; roots, rootlets and fronds arising at any point on the rhizome but roots mainly in clusters where rhizome touches a supporting surface; *sterile fronds* distant on the rhizome and not forming a crown; *stipes* at maturity glabrous or slightly hairy on the adaxial surface, which has one or more grooves; a line of small glands extend on either side of the stipe to the rhizome (often difficult to detect on dried specimens); in cross section the vascular system is complex with ±40 bundles derived from all 3 rings of bundles in the rhizome (Holttum 1968); *sterile lamina* ovate to oblong-lanceolate, pinnate, glabrous and coriaceous; *pinnae* oblong-ovate to lanceolate, acuminate to attenuate and often alternate, sessile to shortly stalked and in some taxa ± articulate at the rhachis; terminal pinna rarely articulate; *pinna margins* finely cartilaginous and serrulate to sharply and sometimes irregularly dentate, usually not green; *veins* arise from the *costa* as a single series of *areolae* sometimes very close to the costa; *lateral veins* arise from the *areolar veins* and free, simple or once- or more rarely twice-furcate, ending near to or at the sclerotic margin; a single marginal gland is usually present on the acroscopic margin close to the pinna base; occasionally two glands are present, one acroscopic and one basiscopic; *fertile fronds* usually with a longer stipe than in the sterile fronds; *fertile lamina* pinnate (bipinnate in *S. tenuifolia*); *fertile pinnae* usually longer than the sterile, ± articulate, slender, (2–10 mm broad), entire to finely toothed, and with narrow, sterile margins either enveloping the sporangia (interpreted here as a false indusium) or spreading, abaxial surface with a sorus on either side of the costa, lacking a true indusium; *sporangia* in linear sori, extending for the length of the pinna or pinnule, the venation with a commissural (areolar) vein and a supplementary system of veins supplying the sori (more easily visible when sporangia are removed). *Spores* (Fig. 1) bilateral, ellipsoid, somewhat hyaline, colourless to pale yellow, papillose with distant tubercles tending to be in parallel rows and with an exceptionally thin, closely adhering perispore.

Cytology: Mehra & Bir (1958) reported the distinct chromosome number of n = 73 for *Stenochlaena* and concluded, on the basis of investigation of a number of morphological characters of *Stenochlaena palustris*, that a phylogenetic relationship exists between *Stenochlaena* and the members of the family Blechnaceae.This report of n = 73 (or 74) is further supported by Tindale & Roy (2002) with 2n = c.146 for material collected from Iron Range in North Queensland, Australia, and by the earlier report of x = 37; 4n = 148 by Manton & Sledge (1954).

Notes: 1. The pioneering study by Underwood (1906) segregated three of the species now recognised as Malesian taxa of *Stenochlaena* into section '*Eustenochlaena*' and the African taxon *S. tenuifolia* into section *Cafraria* (C. Presl) Underw. He also treated the species now segregated into the genera *Lomariopsis* and *Teratophyllum* as sections of his broadly circumscribed *Stenochlaena*. The majority of species, in which both the sterile and fertile fronds are once pinnate, were placed in the section '*Eustenochlaena*' and section *Cafraria* was reserved for the one species with pinnate sterile fronds but bipinnate fertile fronds. However, morphologically, all species share many characters and in some of the once-pinnate taxa occasional mutants will produce a partly bipinnate fertile frond and, less frequently, bipinnate sterile fronds have also been recorded. It is concluded on the basis of comparative morphology, but admittedly in the absence of detailed cytological and molecular analyses, that the separation of section *Cafraria* is not justified.

2. Of the six species accepted as belonging to the genus, only *Stenochlaena areolaris* is a true epiphyte having a relatively specialized and restricted growth habit in the crowns of palms and other plants providing a water reservoir. The other species are hemiepiphytes climbing high on tree trunks but maintaining connection to the soil. All species of *Stenochlaena* appear to require moderately high light conditions in order to produce fertile fronds. All species also require perpetual access to moisture. Based on limited field observations, together with notes accompanying herbarium specimens, those from rainforest environments usually only produce fertile fronds when climbing on trees at the forest margin or on river banks, or when the climbing fern within the forest has reached the canopy.

3. Based on general morphology, it would appear that the loss of an indusium in Blechnaceae probably occurred independently in the genera *Stenochlaena* and *Brainea* and that the two genera arose very early from distinct ancestral elements within this family. This view is supported by the spore morphology which is distinctive in each of these genera. The analyses of Cranfill & Kato (2003), which included both morphological and molecular data (although with only limited sampling of these two genera), provide further support for this hypothesis.

4. There is evidence suggesting that hybrids may occur between several species. *Stenochlaena palustris*, the most widespread and variable taxon, appears to form hybrids with *S. milnei*. It is possible that *S. milnei* is itself of hybrid origin, a view tentatively put forward by Holttum (1971) when he reported that *S. milnei* possessed some characters "almost exactly intermediate" between *S. cumingii* and *S. palustris*.

Biogeography of the genus *Stenochlaena*

The distribution pattern of *Stenochlaena* has parallels in a number of other plant taxa confined to the Old World tropics and sub-tropics. Most species of *Stenochlaena* are present in the Malesian region. *Stenochlaena palustris*, the most widely distributed, best known, abundant, and variable species, occurs throughout Malesia, extending northwest to India, north to other south-east Asian countries, south to northern Australia and east to the Bismarck Archipelago of Papua New Guinea and the south-west Pacific region.

Citations for localities in Papuasia are based on Womersley's (1978) map of "Geographical Regions of Papuasia" Three of the four species in the Malesian region are, from the available evidence, of limited distribution. *Stenochlaena areolaris* appears to be confined to the Philippines and New Guinea, a pattern repeated in a number of ferns and seed plants. *Stenochlaena milnei* is restricted in its distribution to New Guinea, the Philippines, and the Solomon Islands. For *S. cumingii* there are very few collections, these coming from New Guinea, the Philippines, and within Indonesia from the Moluccas. It seems probable that, with further collecting, the distribution may be considerably extended. A recently described additional taxon, *S. hainanensis*, reported from Hainan (Ching & Chiu 1964), although lacking fertile material, is provisionally treated here as a variant within the range of variability accepted for *S. palustris*.

On the Indian Ocean islands, including Madagascar, and in East Africa, the ecological niches occupied by *Stenochlaena palustris* elsewhere are often taken by the tropical and subtropical east African species *S. tenuifolia* (Rakotondrainibe 2002), a taxon with similar ecological requirements but morphologically characterized by having distinctive bipinnate fertile fronds. Cranfill & Kato (2003) mentions that *S. tenuifolia* has been recorded as a garden escape in Florida, U.S.A. in the 1930's. In tropical West Africa, (possibly including Cameroon) and extending south into northern Angola and east into Uganda, *S. mildbraedii* occupies comparable ecological niches. This exceptionally robust and least known species has once pinnate fertile fronds and possesses the largest and most robust sterile fronds reported for the genus. Whether *S. mildbraedii* is really present in Cameroon cannot at this stage be confirmed; I suspect, despite records noting its presence (Tardieu-Blot 1953), that the *Stenochlaena* reported from there may be an additional, as yet undescribed, species. The Cameroon specimens that I have studied are unsatisfactory and it is not possible to be certain that they merit a separate taxon.

Key to the species of *Stenochlaena*

1a. Sterile and fertile fronds once pinnate **2**

1b. Sterile fronds pinnate; fertile fronds almost invariably bipinnate .... **5. *S. tenuifolia***

2a. Aquatic epiphyte; lamina with few sterile pinnae (usually about 7 pairs); fertile pinnae with thin, reflexed sterile margins, 1 mm wide; areolae, created by the veins parallel to the costa, conspicuous .... **4. *S. areolaris***

2b. Hemiepiphytes; lamina usually with 15 or more pairs of sterile pinnae; fertile pinnae with a very slender sterile margin; conspicuous areolae lacking **3**

3a. Apical rhizome-scales elongate, entire, slender, acuminate and mostly deciduous **4**

3b. Apical rhizome scales entire and slender and some almost circular, and appressed **5**

4a. Pinnae coriaceous, margins sharply and irregularly antrorsely toothed .... **6. *S. mildbraedii***

4b. Pinnae chartaceous, margins regularly serrate to finely dentate .... **7. *S.* sp. 'Cameroon'**

5a. Bases of sterile pinnae cuneate; pinnae of fertile fronds 2–3 mm wide; basal sterile pinnae usually articulated .... **1. *S. palustris***

5b. Bases of sterile pinnae broadly rounded to cordate; pinnae of fertile fronds at least 5 mm wide; pinnae often not distinctly articulate **6**

6a. Sterile pinnae rounded at base, some partly articulate; fertile pinnae c. 5 mm wide; spores with prominent tuberculae, partially aligned in rows .... **3. *S. milnei***

6b. Sterile pinnae cordate at base, not articulate; fertile pinnae 7–10 mm wide; spores with continuous or broken ridges and occasional scattered tuberculae .... **2. *S. cumingii***

Southern India, Indochina, Malesia, Papuasia, Northern Australia and Southwestern Pacific Taxa

1. ***Stenochlaena palustris*** (Burm.f.) Bedd., Ferns Brit. Ind. Suppl. 26 (1876); Handb. Ferns Brit. Ind., 421 (1883).

Polypodium palustre Burm.f., *Fl. Indica* 234 (1768); *Lomariopsis palustris* Kuhn, Ann. Mus. Bot. Lugduno-Batavi., 4: 294 (1869); *Chrysodium palustre* (Burm.f.) Luerss., Fil. Graeff., 73 (1871); *Acrostichum palustre* (Burm.f.) Clarke, Trans. Linn. Soc. Bot., 577 (1880).

Type citation: "Habitat in Indiis". **Type:** 'Ceylon' [=Burman, Thes. Zeyl. 100, t. 46] (lecto, see Underwood 1906: 38).

Onoclea scandens Sw., Syn. Fil. 112 (1806) nom. illeg.; *Lomaria scandens* Willd. Sp. Pl. 5, 293 (1810).

Stenochlaena scandens J.Sm., Hook. J. Bot. 3: 401 (1841); *Olfersia scandens* (J.Sm.) Presl, Tent. Pterid. 235 (1836); *Acrostichum scandens* (J.Sm.) Hook. Sp. Fil. 269 (1866) nom illeg., non Raddi.

Pteris scandens Roxb., Hort Bengal. 75 (1814); Calcutta J. Nat. Hist. 4: 505 (1844) **Type:** Rheede, Hort. Ind. Malab. 12: t.35 (see Morton 1974: 375).

Stenochlaena blumeana C. Presl, Epim. Bot. 163 (1851). **Type citation: "**Habitat in sylvis Indiae orientalis ad Tranquebar (Rottler), Javae occidentalis (Blume), Moluccarum (Rumphius)." (Synonymy *fide* Index Filicum, see Holttum, 1969).

Lomaria ? juglandifolia C. Presl, Rel. Haenk. 1: 52 (1825); *Stenochlaena juglandifolia* (C. Presl) C. Presl, Epim. Bot. 164 (1851). **Type:** [Luzon,] *Haenke s.n.* (PR, n.v.).

Stenochlaena fraxinifolia Presl, Epim. Bot. 164 (1851); *Stenochlaena scandens* var., J.Sm., Hook. J. Bot. 3: 401 (1841). **Type:** Philippines, Negros, *Cuming 347* (PR, n.v.).

Stenochlaena laurifolia C. Presl, Epim. Bot.164 (1851). **Type:** Philippines, Luzon, *Cuming 226* (PR, n.v.; excl. dupl. BM, K).

Etymology: from the Latin, 'paluster' referring to the swampy places from which the original collections were made.

Published illustrations: Hooker, Gen. Fil. pl. 105B (1842) (as *S. scandens*); Beddome, Ferns of Southern India, pl. 201 (as *S. scandens*) (1863); Tardieu-Blot, Aspléniacées Tonkin, pl. 47, f. 1 (as *S. palustris*) (1932); Nayar & Devi, fig. 52 (spore as *S. palustris*) (1964); Holttum, Rev. Fl. Malaya, 2: f. 241 (1968); Zamora P.M. & Co L, Guide Philip. Flora & Fauna 2: 52, f. 44 (1986); A.G.Piggott & C.J.Piggott, Ferns of Malaysia in Colour, 410 (as *S. palustris*) (1988); S.B. Andrews, Ferns of Queensland, 87, f. 7.1c (1990) (*as S. palustris*); Kramer & Green, fig. 25 A–E (1990); Chambers & Farrant, Fl. Australia 48, fig 123 A, B. (1998).

Rhizome extensive, indeterminate, smooth, scrambling and climbing (sometimes floating when growing over river and lake banks), stramineous to brown, 0.5–0.7 cm diameter, with peltate ± entire, mostly round persistent scales and green to red-brown acuminate scales that are closely appressed to the surface and mostly caducous except for areas giving rise to roots, clusters of rootlets and dimorphic fronds. *Sterile fronds* variable in size, mostly 25–85 (–175) cm × 9–30 cm wide; *stipes* 10–30 cm or more, stramineous to brown, glabrous or with a few persistent peltate scales; *lamina* ovate or oblong-ovate in larger specimens; *pinnae* 4–15 pairs, usually widely spaced, all or some articulated to the rhachis, sessile to shortly stalked, ovate to lanceolate, acuminate to frequently attenuate, entire to finely toothed or apex more markedly toothed if attenuate; base almost entire, a single *gland* (rarely 2) usually present either at the base of the pinna margin or on the short pinna stalk; lateral veins simple or once-furcate, arising from areolar veins closely parallel on either side of the costa; *terminal pinna* usually larger than the sub-terminal pairs, in most specimens lacking a gland and not articulated to the rhachis. *Fertile fronds* about as long as sterile fronds but with stipe longer; *pinnae* 8–25 cm, up to twice the length of those of the sterile lamina, 2–3 mm broad; approaching maturity the margins of the *fertile pinnae* appear to slightly envelop the linear sori but at maturity the lamina reflexes and the sori appear acrostichoid. Fig. 2.

Spores bilateral, and ornamented with short round projections more or less in rows and almost colourless but in masses have a pale lemon yellow tinge; *perispore* very thin, closely enveloping, difficult to differentiate from the spore wall. Fig. 1d.

Chromosome number: x = 74 (base number may be 37; Kramer & Green (1990), a number occasionally also reported for *Blechnum*). Mehra & Bir (1958) illustrate a spore mother cell at meiosis with 73 bivalents, while Manton (1954) and Manton & Sledge (1954) have suggested that $n = 70–80$ and most probably $n = 74$ and $2n =$ c. 148.

Distribution and habitat: extending from India through Myanmar (Burma), south and south-east Yunnan in China, Thailand, Laos, Vietnam through Malesia east to the Solomon Islands and south to northern Australia, and in the Pacific southeast as far as the islands of Fiji, (recorded by Brownlie (1977) on three islands: Viti Levu, Vanua Levu and Taveuni) (Fig. 3). This species is also reported present on Samoa and Tonga (Holttum 1971). *Stenochlaena palustris* is a very adaptable species colonising margins of hot springs and mangroves in coastal environments; in some areas forming extensive floating mats on fresh water at forest edges. This species is found growing in permanently damp open places in tropical and subtropical lowland areas especially on forest margins on the ground and climbing high up a wide range of trees and palms and also abundant in secondary forest. It has also been reported as a weed in rubber and oil palm plantations and in abandoned gardens.

Selected specimens examined: THAILAND: Bangkok, Straits of Malacca, Pulau Labang, *Smith 995* (SING). **MALAYSIA:** Penang: Penang Waterfall Gardens, *Holttum s.n.* (SING); Pahang: TeKah, *Holttum 24678* (SING); near Tamerloh, *Holttum*

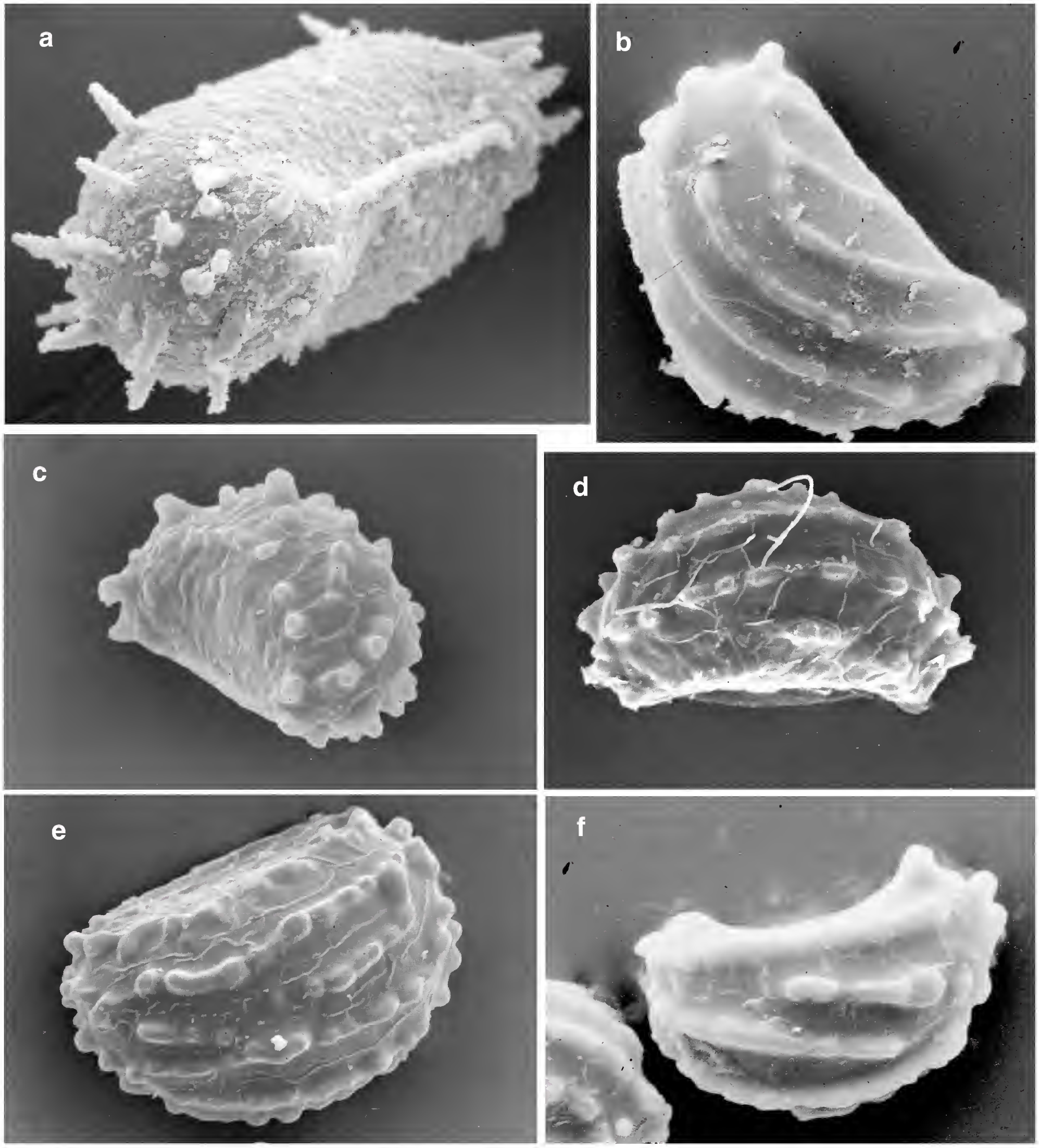

Fig. 1. Scanning electron micrographs of *Stenochlaena* spores. **a,** *S. areolaris*; **b,** *S. cumingii*; **c,** *S. milnei*; **d,** *S. palustris*; **e,** *S. tenuifolia*; **f,** *S. mildbraedei*.

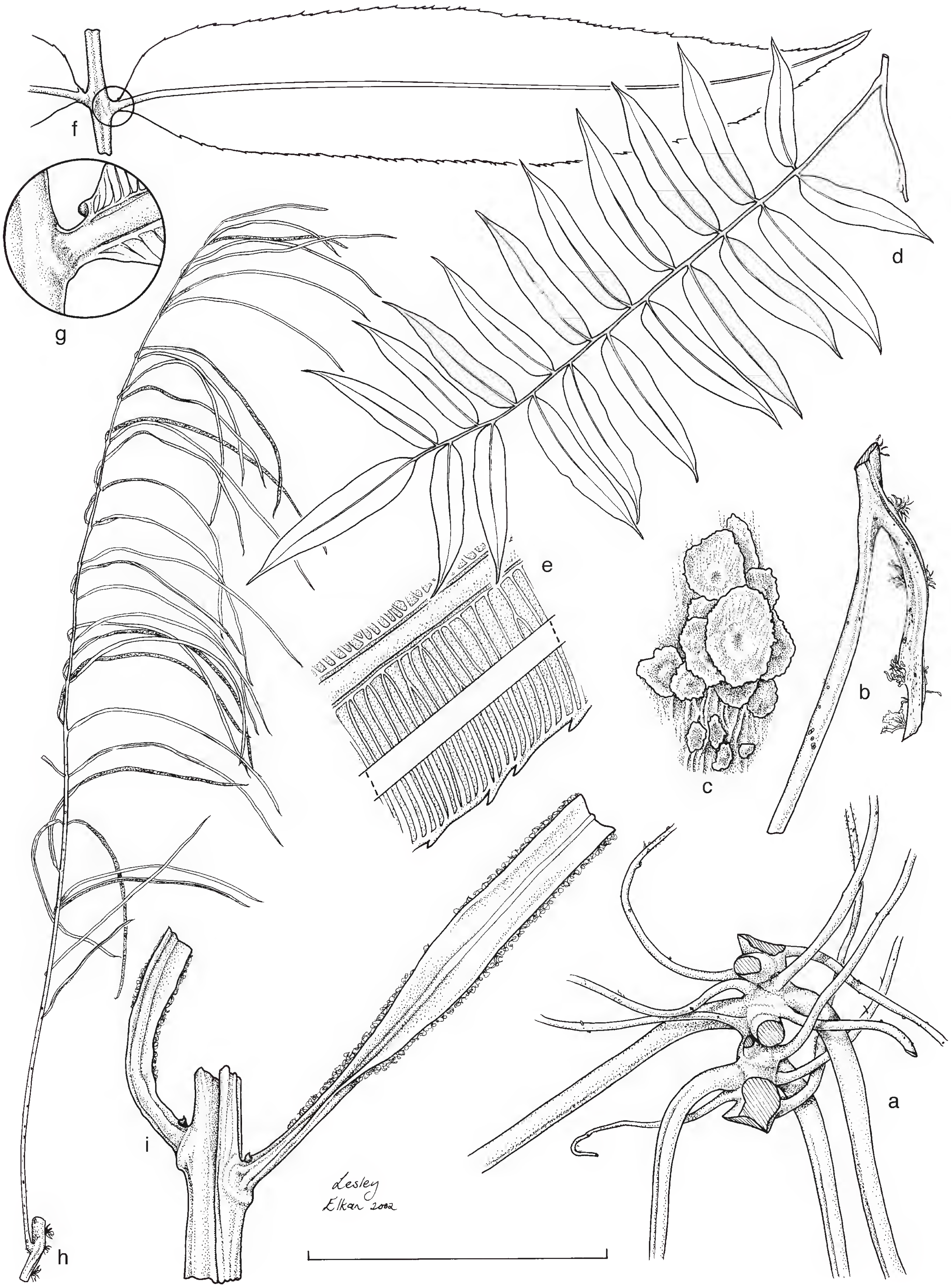

Fig. 2. *Stenochlaena palustris* (Burm.f.) Bedd. **a,** mature rhizome showing roots and stipes; **b,** rhizome showing characteristic branching and clusters of rootlets; **c,** peltate scales on the rhizome; **d,** sterile frond; **e,** detail of abaxial surface of a sterile pinna showing serrate margin and the lateral veins arising from the areolar vein closely parallel to the costa; **f,** rhachis and sterile pinna; **g,** abaxial view showing detail of articulation of pinna at the rhachis and the gland at the base of a pinna; **h,** fertile frond; **i,** adaxial view showing detail of base of fertile pinna, articulation at the rhachis and the gland. Scale bar: a, b = 7.5 cm; c = 0.4 cm; d, h = 20 cm; f = 5 cm; e, g, i = 1.2 cm. Specimens: a, *M. Raciborski s.n.* (L 0440437); b, h, i, *L.J. Brass 6441* (L 0441454, 55); c–g, *L.J. Brass 7648* (L).

24590 (SING); Selangor: Pulau Angsa, Kuala Selangor, *Wyatt Smith 71140* (SING); Klang Road, *Strugell, 13995*bis (L); **SINGAPORE:** Singapore Botanic Gardens, *Holttum s.n.* (SING); Kuala Trengganu *Hume* (SING). **PHILIPPINES:** Luzon: Labo, *Price 360* (L, NSW); Leyte: *Ramos 15311* (L, NSW). **INDONESIA:** Sumatera Utara: *Iwasuki et al 4532* (L, SING); Lampung: Enggano *Lutjeharms 4060* (L, SING); Java, *M. Raciborski s.n.* (L); Jawa Barat: *Holstrooyd 742* (L, SING); Bali: *van Steenis 7570* (SING). **PAPUA NEW GUINEA:** East Sepik: 'Nungrum', *Leach 34243* (L, NSW); Amba, *King s.n.* (NSW); Daru I. *Brass 6441* (L); Lake Davimbu, Middle Fly River, *Brass 7648* (L). **AUSTRALIA:** Northern Territory: Darwin and Gulf: Alligator River, *Bishop 827* (L, NSW, SING); 15 km SE of Darwin *Chippendale 6194,* (L, NSW, SING); Gove, *Croat 52473* (L, MO, NSW, SING); Howard Springs, *Beauglehole 10964* (L, NSW, SING); Arnhem Land, *Specht 1126* (L, NSW); Kakaku National Park, *Tindale 10002 & Nunns* (L, NSW); Bickerton I.,Gulf of Carpentaria, *Specht 452* (L, NSW); Cobourg Peninsula, *Letts 8316* (L, NSW); Melville I., *Briggs 8096* (L, NT, NSW). Western Australia: Gardner: South of Cockburn Range, Kimberleys, *Beauglehole 47133* (NSW, SING). Queensland: Cook: Daintree, *Jacobs 6183* (L, NSW).

Nomenclature and Typification: 1. Underwood (1906) was the first person to use this binomial and to cite *Polypodium palustre* Burm.f. as a synonym. Morton (1974) suggested that Beddome (1876) did not validly publish the combination and attributed it to Underwood, but it is clear that Beddome did make the combination, despite the vague, indirect reference to the basionym. Underwood was also the first to indicate a type for *Polypodium palustre*. His designation 'Type from Ceylon' can only be interpreted as a reference to the plate in Burman's *Thesaurus Zeylanicus* cited above.

2. Underwood (1906) was also the first to point out that Swartz was responsible for a "Change of Burmann's specific name without warrant." Swartz cited *Polypodium palustre* as a synonym, thus rendering his binomial illegitimate. Swartz has often been cited as parenthetic author for the binomial *Stenochlaena scandens* but John Smith did not cite Swartz, rather he cites 'Acrostichum scandens *Linn.*' as a synonym although Linnaeus apparently never published this name. The type of *Stenochlaena scandens* J.Sm. is difficult to determine. Smith's mention of Linnaeus might be taken as an indirect reference to p. 200 of his pre-starting point *Flora zeylanica* and to his citation of 'Burm. zeyl. 100. t. 46.' there, under the first entry on the page; otherwise, one of the three Cuming collections he cites would have to be chosen as lectotype. The first option is preferable.

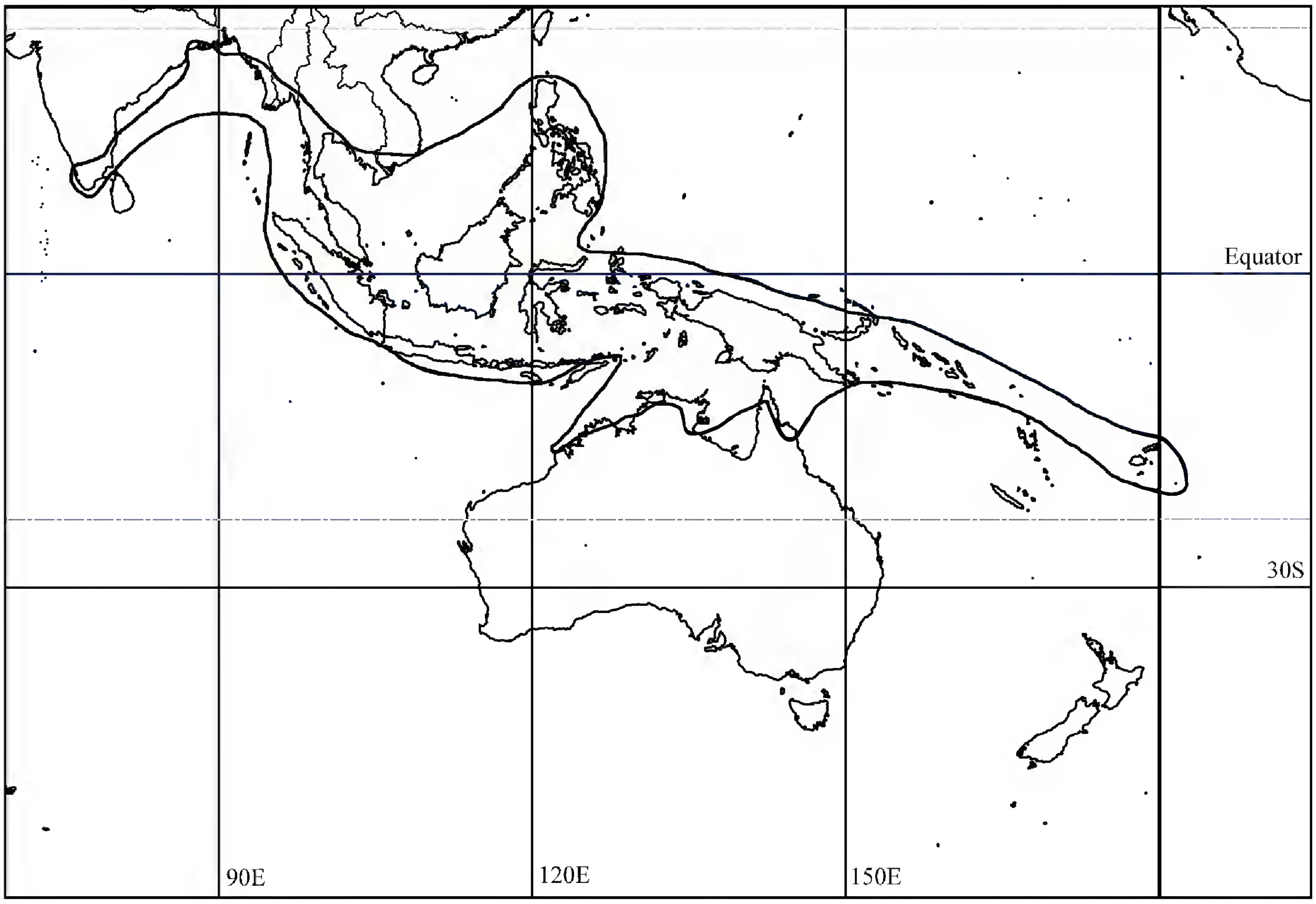

Fig. 3. Distribution map for *Stenochlaena palustris* (Burm.f.) Bedd.

3. Holttum (1932, 1939) adopted Presl's name *Stenochlaena laurifolia* following Hooker's concept (1864), accepting it as a distinct species. Later he was able to examine Presl's types and found that the Prague specimens of the type, *Cuming 226*, were "within the normal limits of variation" of *Stenochlaena palustris* (see Holttum 1969: 51, 52) and, therefore, not conspecific with specimens at BM and K, bearing the same number. Rather, these specimens were in agreement with Hooker's application of the name. Holttum (1971) subsequently published a new name for the taxon, *Stenochlaena cumingii*, typified by the Kew specimen of *Cuming 226* (see further note below, under *S. cumingii*).

Notes: 1. The sterile pinnae are variable in shape and size. At least some of this variation is a response to the position of a frond on the extensive rhizome of this liana. Unfortunately, the information on the position on a plant from which herbarium material has been collected is rarely given. I have not found any collection that gives a full representation of the variation in morphology to be found in the various zones inhabited by a single plant.

2. Two specimens collected by *van Daalen 460a* (L 0441508, L 04415090) are labelled *Stenochlaena palustris* f. *subintegerrima* Ros. (det. by Rosenstock, presumably unpublished) and annotated 'Vide Enumerationem Revisionis Filic. Palaeotrop. ex bibliotheca Ludg. Ba. No 13,679'. The sterile pinnae have margins tending to be entire at least in their basal half. This is a commonly observed phenomenon and is not worthy of formal recognition.

3. Another herbarium specimen (L 0441506) is labelled *Stenochlaena palustris* v. *pubescens* Ros., (det. by Rosenstock, 1922; probably also ined.) and is annotated 'Vide Enumerationem Revisionis Filic. palaeotrop. in Bibliotheca Herb. Lugd. Bat: No. 19191.' It has the abaxial surfaces of the stipe, rhachis, costae and pinnae surface densely pilose with very fine short, unicellular hairs less than 0.4 mm in length; on the pinna surface these arise from the lateral veins as well as from the areas between the veins. This appears to be a distinct variety but I have only seen this single, incomplete specimen.

4. A further specimen (L 0441504) is glabrous and labelled *Stenochleana palustris* var. *inermis* Ros. (det. by Rosenstock, 1922; probably also ined.) and is annotated 'Vide Enumerationem Revisionis Filic. palaeotrop. ex bibliotheca Herb. Lugd. Bat. No.18155.'

5. Occasional specimens produce bipinnate or at least partly bipinnate sterile fronds (see, for example, *Hennipman s.n.* [L 0441491] ex cult. Leiden), the pinnules of which are slender. However these pinnules always show, on careful examination, the areolae very close to parallel to their costae.

6. Holttum (1968) reports that the characteristic 'pinna gland' on the rudimentary basal pinnae are active secretory organs when the frond is very young and become blackened and shrivelled on older fronds (Troll 1932).

7. Locally known as *hagnáya* at Taytay, Palawan, in Manila as *diliman*. The tough climbing stems are brought to Manila in large quantities, and because of their durability in salt water, are extensively used by the local people for tying together the parts of bamboo fish traps'. Zamora & Co (1986) also list the local name '*lanas*' but without mentioning a particular region.

2. *Stenochlaena cumingii* Holttum, Amer. Fern J. 61: 122 (1971).

Type: Luzon, *Cuming 226* (holo: K; iso: BM; excl. dupl. PR, see note under *S. palustris*); see further note below.

Stenochlaena scandens var. β, J.Sm., J. Bot. (Hooker) 3: 401. 1841. **Type:** Philippines, Luzon, *Cuming 133* (K, L).

Stenochlaena laurifolia C.Presl, *sensu* Holttum, Gard. Bull. Str. Settl. 5: (1932) see note below.

Literature: Holttum, Gard. Bull. Str. Settl. 9: 140 (1937); Copeland, Fern Fl. Philippines, 428, (1960).

Published illustrations: Holttum (1932) as *S. laurifolia,* plate 18, fig.18.

Etymology: honours Hugh Cuming (1791–1865), who collected the type material from the Philippines on his third voyage to the Pacific region in his yacht *Discover*.

Rhizome robust, to 30 m, up to 2 cm diameter, with several large central vascular bundles and c. 2 outer whorls of numerous small bundles, (essentially similar in arrangement to those of *Stenochlaena palustris*), scales not observed; *stipes* robust, vascular tissue very complex with over 100 vascular bundles; *sterile lamina* oblong-ovate; *sterile pinnae* 2.5–3.2 cm wide, 12–25 cm or more long, broadest near their bases which are distinctly rounded to slightly cordate, not articulated, acuminate, margins strongly toothed, apex shortly attenuate, coriaceous, *costal areolar veins* giving rise to single or once furcate lateral veins; lowermost pinnae robust and usually serrate to almost dentate, almost sessile and rounded to sub-cordate and spaced on the rhachis,

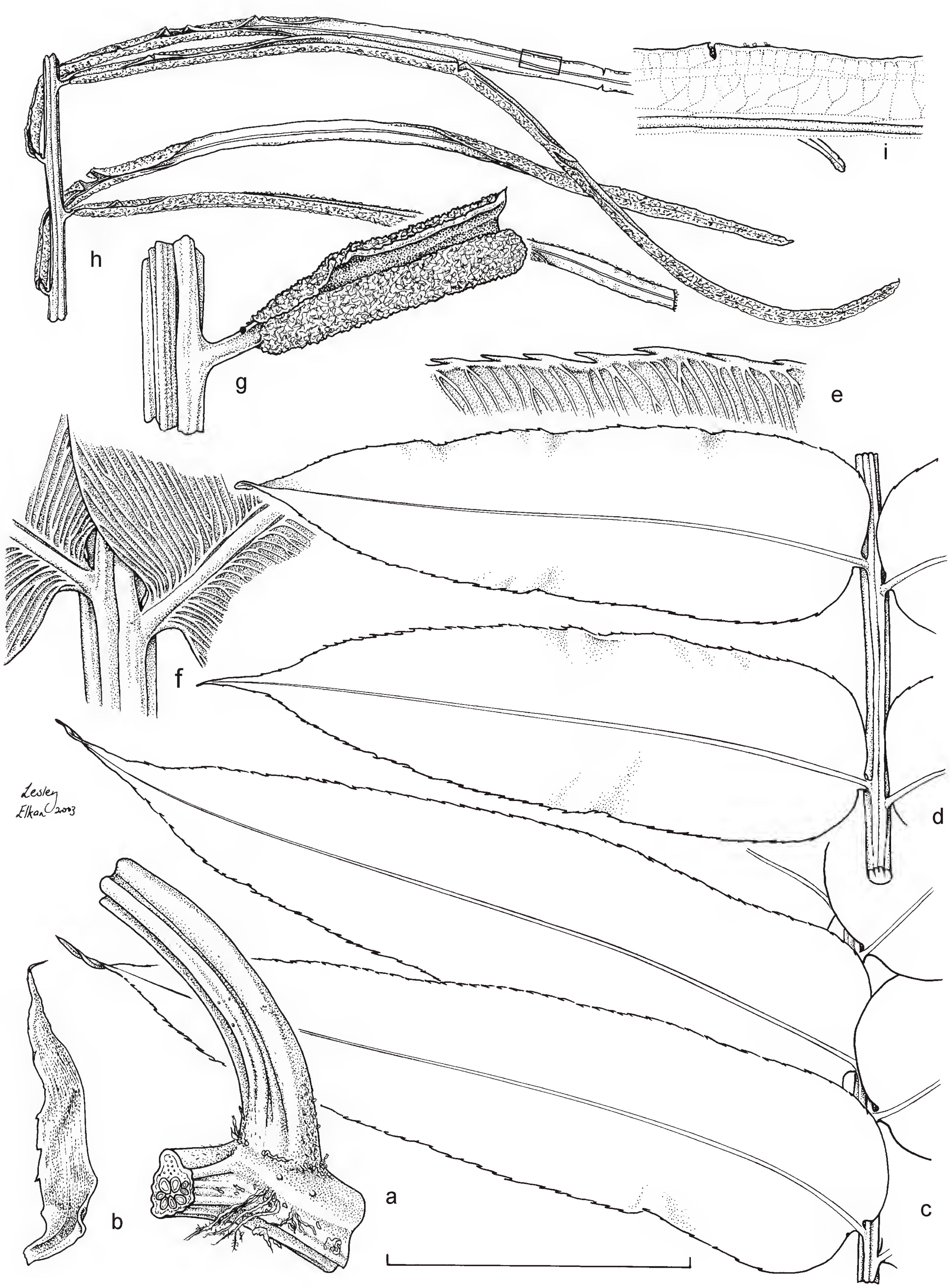

Fig. 4. *Stenochlaena cumingii* Holttum **a,** rhizome section and junction with base of stipe; **b,** rhizome scale; **c,** basal sterile pinnae; **d,** mid-region sterile pinnae; **e,** detail sterile pinna margin; **f,** adaxial view sterile pinna attachment to rhachis, lateral veins arising from areolae closely parallel to the costa; **g,** fertile pinna arising from rhachis, showing rolling of the lamina; **h,** fertile pinnae from mid-frond region **i,** venation abaxial surface of fertile pinna showing the network of lateral veins originating from the commissural vein parallel to and close to the costa. Scale bar: a, c, d = 6 cm; b = 0.6 cm; e, i =1.5 cm; f, g = 2 cm; h = 10 cm. Specimens: a, b, *Beguin 1170* (L 0440287); c–f, *Cuming 133* (L 0440273); g–i, *J.R.Croft 1703* (L 0441486).

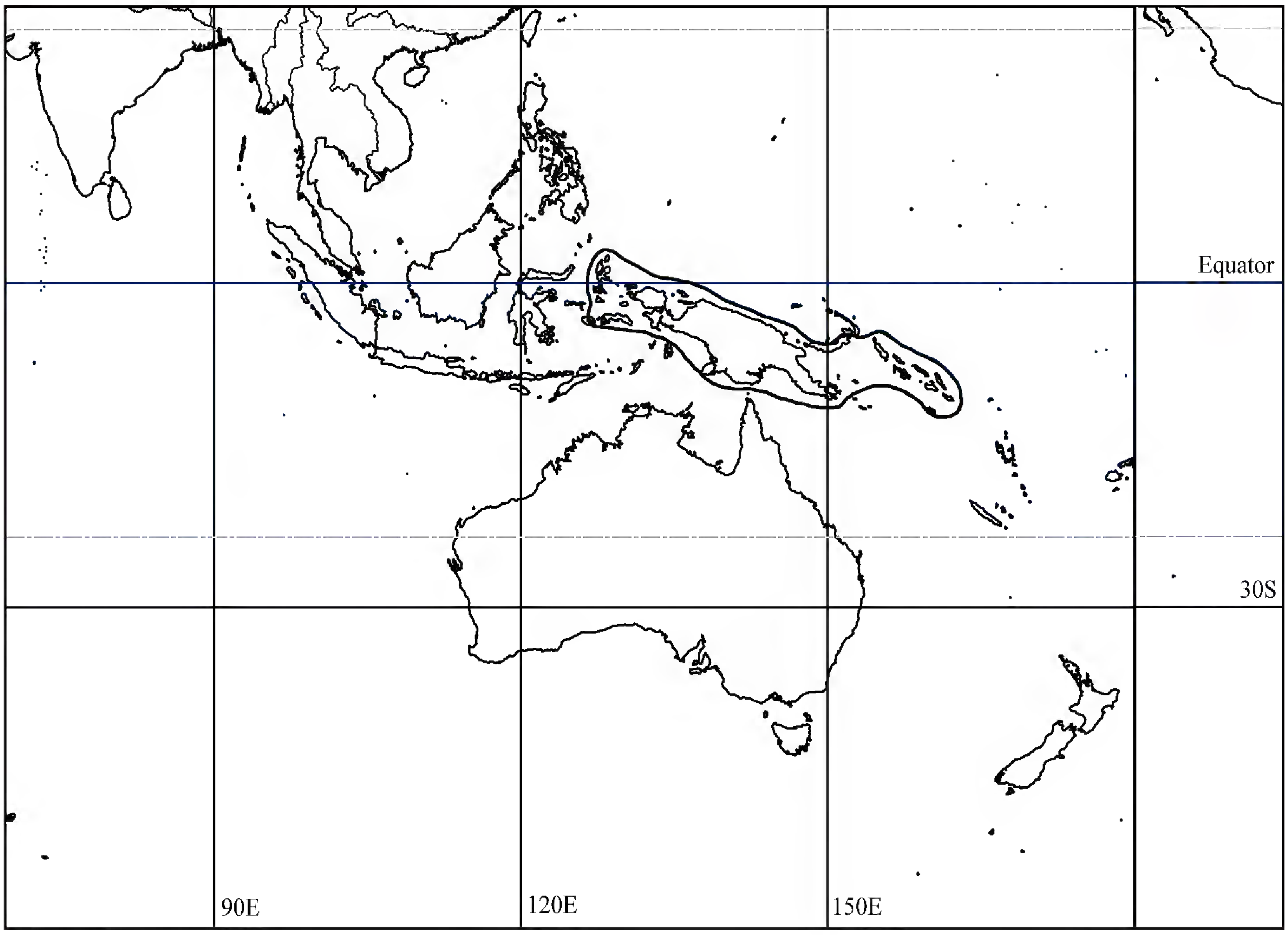

Fig. 5. Distribution map for *Stenochlaena cumingii* Holttum.

towards the lamina apex the pinnae decrease in length, become shortly stalked and increasingly imbricate and cuneate at their bases and less serrate than lower pinnae; a *gland* is present on the acropetal margin at the base of the lateral pinnae (but sometimes difficult to detect), *terminal pinna* usually lacking a gland. *Fertile fronds* with *fertile pinnae* mostly shortly stalked, up to at least 30 cm long, 7–10 mm wide, with a network of sub-costal areoles and anastomosing veins not extending to the sometimes finely toothed margins which are reflexed at maturity; veins can be observed on the adaxial surface showing numerous anastomoses. Fig. 4.

Spores pale yellow, with numerous blunt spiny projections along elongate parallel ridges. Fig. 1b.

Distribution and habitat: extending from the Philippines, through Maluku to Papua New Guinea (Holltum 1971), possibly occurring in the Solomon Islands, especially on the edges of forest habitats. Fig. 5.

Specimens examined: PHILIPPINES: Luzon: *Cuming 226* (K, BM); Cuming 133 (L 0440273). **INDONESIA:** Maluku: Ternate, *Beguin1170* (L 0440287).

Note: 1. Hooker (1864) accepted *Stenochlaena laurifolia* C. Presl as distinct. Holttum (1932, 1939) followed Hooker in this, but later discovered that Presl's type, *Cuming 226*, was not conspecific with specimens bearing the same collector's number at K and BM (see Holttum 1969: 51, 52). Holttum attempted to address this by publishing the nom. nov., *S. cumingii*, but Morton (1970: 123) pointed out that this did not constitute valid publication of the name, which would require a Latin description and designation of a type. Holttum (1971) remedied this and designated the Kew specimen of *Cuming 226* as holotype.

2. Very few specimens were available for study and a number of characters were poorly preserved or missing, e.g. rhizome scales. The species has been reported from Papua New Guinea but no specimens were located.

3. *Stenochlaena milnei* Underw., Bull. Torrey Bot. Club 33: 38 (1906).

Type: Solomon Islands., *Milne 518* holotype: K; paratypes: *Milne 590*; New Guinea, *Honkmann* s.n. K; Admiralty Is., *Moseley s.n.* (K).

Stenochlaena juglandifolia sensu Holttum, Gard.Bull.Str. Settl. 9: 139 (1937).

Literature: Copeland, Fern Fl. Philippines 428 (1960) as *S. juglandifolia*; *non* C. Presl, Epimel. 164 (1849).

Etymology: honors William Grant Milne, a Scottish botanist and horticulturist who collected the original specimens of this taxon on the voyage in the 18th century of the sailing ship 'HMS Herald'.

Rhizome climbing and similar to that of *S. palustris,* symmetry radial; scales peltate to linear-acuminate, 4–5 mm long, 1 mm wide at base, entire to irregularly toothed and with a peltate attachment. *Sterile fronds* large, with glabrous stipes, vascular bundles numerous (usually more in number than in *S. palustris*); *sterile lamina* oblong acuminate to oblong-ovate, ± 10 pairs pinnae; *sterile pinnae* large and robust, in the mid-lamina region 15–25 cm long, 2.5–3 (–3.5) cm wide, oblong and attenuate, mostly not distinctly articulate to the rhachis, broadly rounded and entire at their bases but remaining margins cartilaginous and conspicuously toothed; terminal pinna not much larger than the subtermina. *Fertile fronds* with both *stipe* and *fertile lamina* of about the same dimensions and outline as for the sterile frond; *fertile pinnae* as long as or longer than sterile pinnae, at least 5 mm wide. Fig. 6.

Spores with tubercles emerging from irregular discontinuous ridges. Fig. 1c. Holttum (1971) and Tryon & Lugardon (1990) illustrated a spore from a New Guinea specimen (*Clemens 3125*), indicating fewer tubercles (than in Fig 1c) that are randomly distributed on irregular discontinuous ridges.

Distribution and Habitat: occurs in closed forest in humid habitats. It is less frequent in collections, probably indicating it is less common in occurrence. It is reliably recorded from the Philippines, Indonesia (Maluku), Papua New Guinea and Solomon Islands. Fig. 7.

Specimens examined: PHILIPPINES: Luzon: Mt. Makiling, Laguna, 420 m, *Price 476* (L); Luzon, *Elmer 16253* (L); *Cuming 133A* (L). **INDONESIA:** Maluku: Ceram, *de Vriese,.Teijsmann s.n.* (L 0440288, 0440289); Hunitetu, Kairatu, 350-400 m, *Kato et al c-2184* (L, BO.); Trail to Mt Totaniwel, Kecamatan District, Kairatu,120 m, *Kato et al C-13290* (L, BO), N of Piroe *Rutten 1914* (L); Hunitetu, *Kato et al c-2194* (L); Ternate, Sasa-ketjil, *.Beguin 1170* (L); Tehoru, *Kato et al c-13760* (L, BO); Trail from Wae River to Tehoru, *Kato et al c-11742* (L, BO); West New Guinea,Vogelkop: (probably) Forest Reserve Tafelberg, *Versteegh & Vink BW 8398* (L). **PAPUA NEW GUINEA:** West Sepik: N. slope of Bewani Mts. *Croft 1703B* (NSW) & 1703 (one sheet of two at L, A, CHR); Papuan Islands: Salamo, Fergusson I. *Streimann & Lelean LAE52572* (L).

Notes: 1. Holttum (1937) pointed out that *Stenochlaena milnei* (as *S. juglandifolia*) is intermediate in a number of characters between *S. palustris* and *S. cumingii* (*S. laurifolia*) including shape of base of sterile pinnae, articulation of the pinnae, width of fertile pinnae, number of vascular bundles in the stipe and the distribution of tubercles on the spores.

2. Holttum (1971) confirmed that *Stenochlaena milnei* is 'almost an exact intermediate between *S. palustris* and *S. cumingii*' indicating that *S. milnei* may be of hybrid origin.

3. *Stenochlaena milnei* is a very robust fern, sometimes confused with large specimens of *S. palustris.* However in *Stenochlaena milnei* the rhachis ridges are more complex and support much larger and more consistently oblong pinnae and more conspicuously toothed pinna margins the teeth closer together especially towards the pinna apices; pinnae are often with attenuate apices sometimes with the appearance of drip tips. Fertile pinnae of *S. milnei* at maturity are very much more robust than those of *S. palustris.*

4. Some specimens that are intermediate in their morphological characters between *Stenochlaena milnei* and *S. palustris* are probably backcrosses to the parental species. e.g. *McKee 1643* (NSW) from Betivatu, British Solomon Is. (Guadalcanal) and *Gideon LAE78512* (L, NSW) collected from Mt Bagana, Torokina, North Solomons Province (Bougainville) and *Hennipman 5689* from Sulawesi Tengah (L) are specimens that would appear to be either the result of dominance of *S. milnei* characters or the product of further backcrossing to *S. milnei*. A specimen from Sirinumu (Central, Papua New Guinea), *R. Schodde 2986* (L) is intermediate in a number of characters and is also possibly a hybrid with *S. palustris.*

5. Holttum (1971) reported that *S. milnei* is the common species in the vicinity of Lae (Morobe), Papua New Guinea whereas *S. palustris* is not common.

6. Underwood's original description (1906: 38) was based on fragmentary specimens at K. Although additional material available for the present study has made a more complete description possible, the specimens available lack some details. Pinna variation indicates a wide range in the degree of stalk development and this may, with more carefully documented collecting, be indicative of a response to the position of a sterile frond on the plant; this is possibly an important detail not noted on any of the specimens examined.

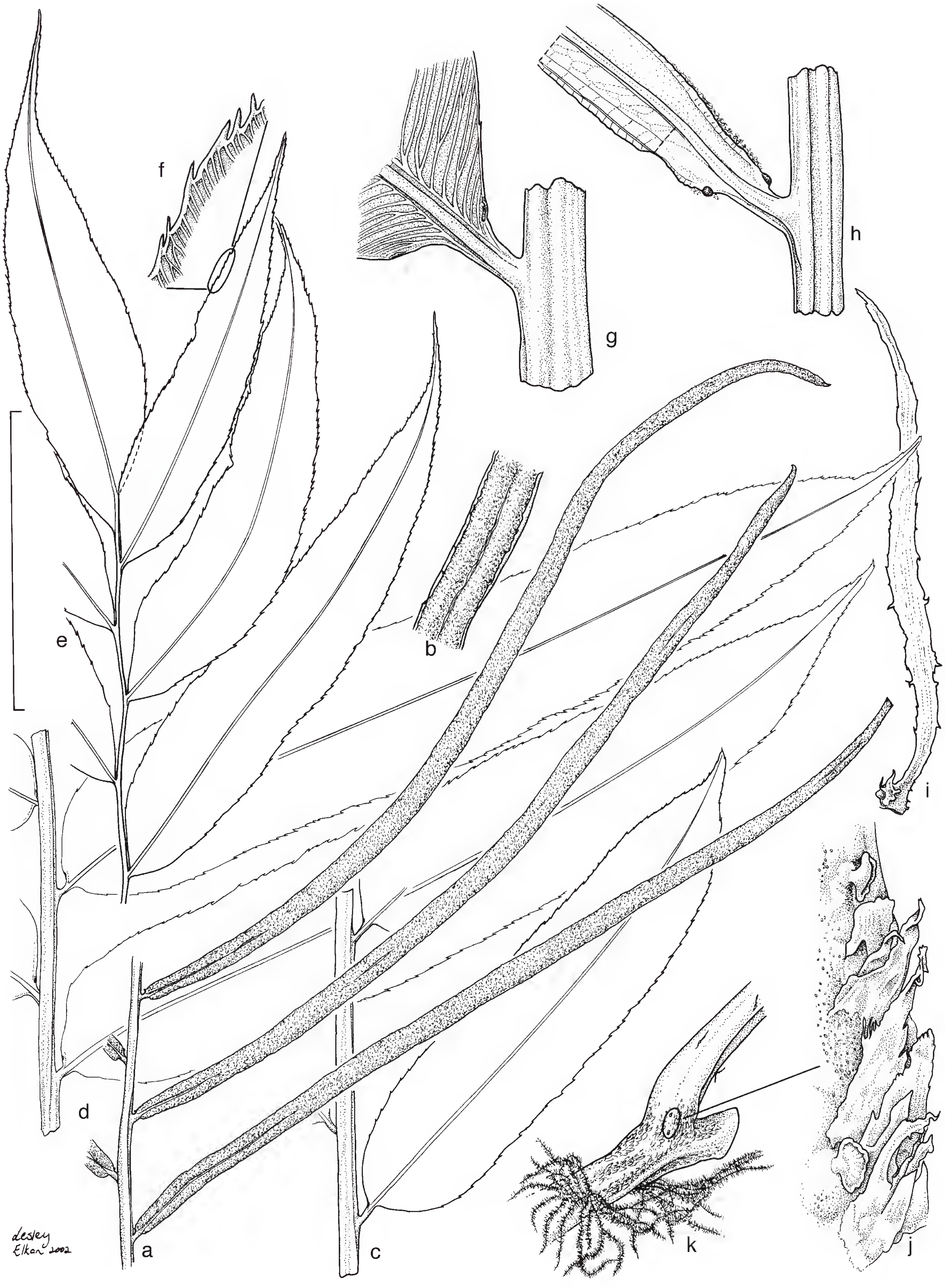

Fig. 6. *Stenochlaena milnei* Underw. **a,** mid-region of fertile lamina, abaxial surface; **b,** abaxial detail of pinna from base of fertile lamina; **c,** sterile pinnae from basal region; **d,** sterile pinnae from mid-region; **e,** sterile pinnae from apex of lamina; **f,** slightly irregular serration detail of sterile pinna margin; **g,** detail of sterile pinna base; **h,** fertile pinna bases showing glands venation in dissected region; **i,** detail rhizome scale; **j,** rhizome scales in situ; **k,** detail of rhizome and typical clustering of roots. Scale bar: a, b, c, d, e & k = 8 cm; f, g, h =2 cm; i, j = 0.6 cm. Specimens: a–c, f, g, *J.R. Croft LAE 373938*, L 0440309; d, e, *J.R. Croft 68280* L 0440308; f, g, *J.R. Croft* L 0440309; h–k *L.J. Brass 27581* L 0440311.

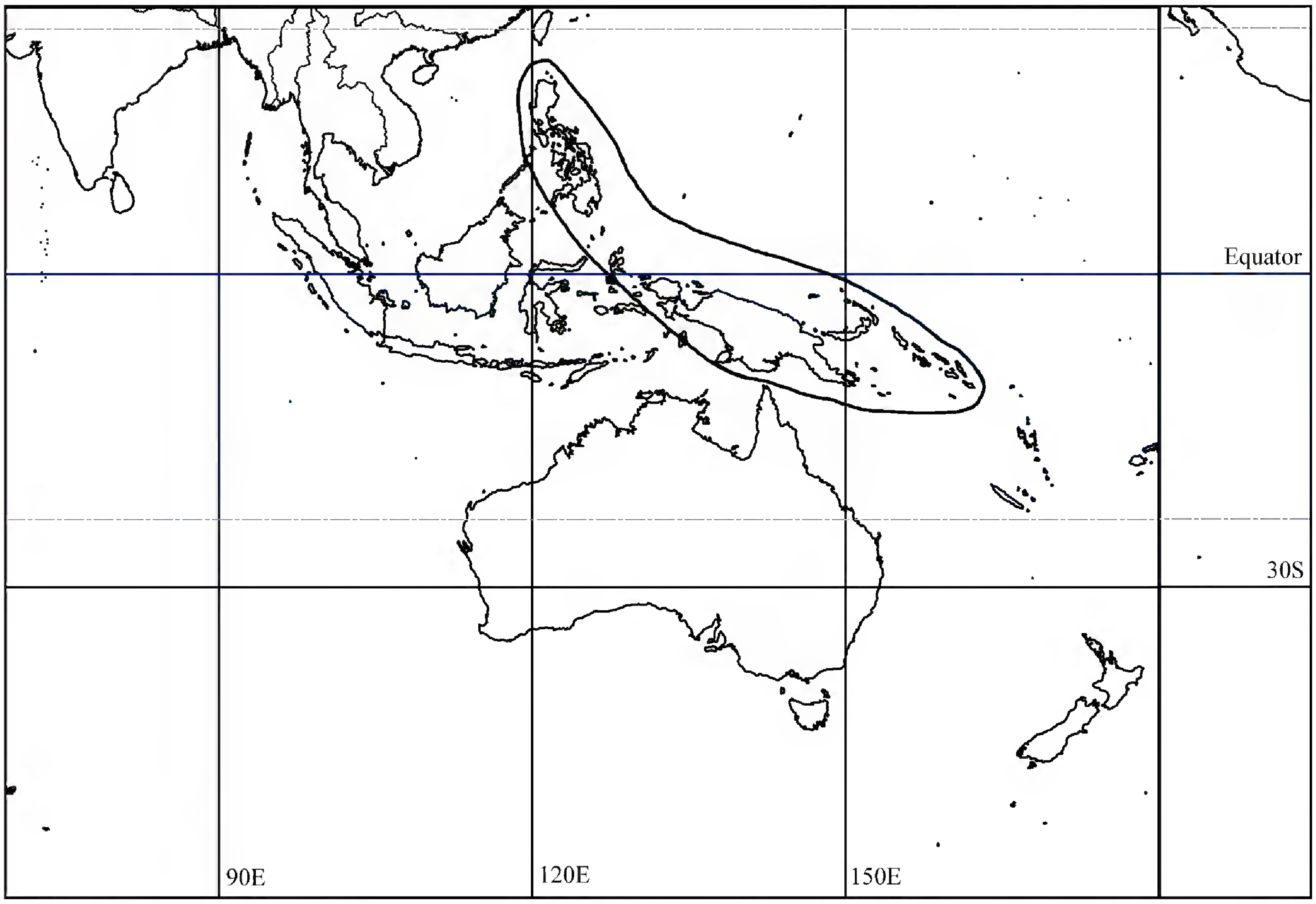

Fig. 7. Distribution map for *Stenochlaena milnei* Underw.

4. *Stenochlaena areolaris* (Harr.) Copel. Philipp. J. Sci. 2C, 406 (1908); Fern Fl. Philippines 427(1960).

Lomaria areolaris Harr., J. Linn. Soc. Bot. 16: 28 (1877); *Spicanta areolaris* (Harr.) Kuntze Rev.Gen. Pl. 822 (1891); *Blechnum areolare* (Harr.) C. Chr. Ind., 150 (1905.

Type: PHILIPPINES: Luzon: Mount Mahayhay, *Steere*, 'Growing among the leaves of a *Pandanus*' (holo: MICH?, n.v.).

Published illustrations: Holttum (1932: 252, fig. 3) drawing of spore.

Etymology: from the Latin 'areola' which describes the often conspicuous spaces defined by the vein pattern on the sterile pinnae, especially the shapes created by the commissural veins parallel on either side of the costa (Fig. 8 d, i).

Crown epiphyte with *rhizome* to about 30(– 90) cm long, smooth, buff-coloured, relatively slender 1–2.5 mm diameter often twisted, and giving rise to slender branches (0.5–1 mm diameter), each terminated by a tuft of minute, linear-acuminate, red-brown almost entire, and somewhat clathrate scales 2 mm long, 0.5 mm wide. S*terile fronds* with *stipes* smooth, glabrous, stramineous and up to 25 cm; *sterile lamina* to 30 cm, ovate to oblong-lanceolate, coriaceous. S*terile pinnae* few, typically up to 7 pairs spaced, ovate, acuminate, finely serrate, sessile to sub-sessile (up to 10 cm long, 2.2–3 cm wide on mature specimens); *lateral veins* single or once furcate, arising from *areolae* less than 1/6 width of a pinna and usually more distinct on adaxial surface; *sterile pinnae* with bases rounded to sub-cordate; *terminal pinna* as large or larger than sub-terminal pinna; usually on any one plant there are also smaller fronds with fewer pinnae, 2.5 cm long, 0.8 cm wide. *Fertile fronds* with *stipes* 50 cm long or more, significantly longer than the stipes of sterile fronds; *fertile pinnae* 7–9 pairs, to 100 mm long, 3–4 (– 6) mm wide with margin thin, 1mm wide, forming a false indusium during early development of sporangia and becoming reflexed at maturity when sporangia appear to cover the abaxial surface. Fig. 8.

Spores relatively elongate, tubercles or spines are slender and longer than in other members of the genus and are usually more densely clustered at the polar ends which tend to be flattened. Fig. 1a.

Fig. 8. *Stenochlaena areolaris* (Harr.) Copel. **a,** habit; **b,** detail of base of sterile pinna showing glands; **c,** sterile pinna base showing the articulated junction at the rhachis; **d,** sterile pinna showing areolae parallel to the costa giving rise to the lateral veins; **e,** base of fertile pinnae abaxial surface showing the gland; **f,** fertile pinnae adaxial view; **g,** fertile lamina abaxial surface; **h,** roots arising from rhizome; **i,** juvenile plant showing rhizome, roots and juvenile frond with three pinnae with conspicuous areolar veins. Scale bar: a = 12 cm; b = 2 cm; c = 1 cm; d = 4 cm; e, f = 1 cm; g, h = 6 cm; i = 4 cm. Specimens: a, b, *M.G. Price 285* (NSW); c, d, i, *M.G. Price 578* (L); e–g, *J. Croft* 1110 (NSW); h, *A.D.E. Elmer 7961*(L L044026).

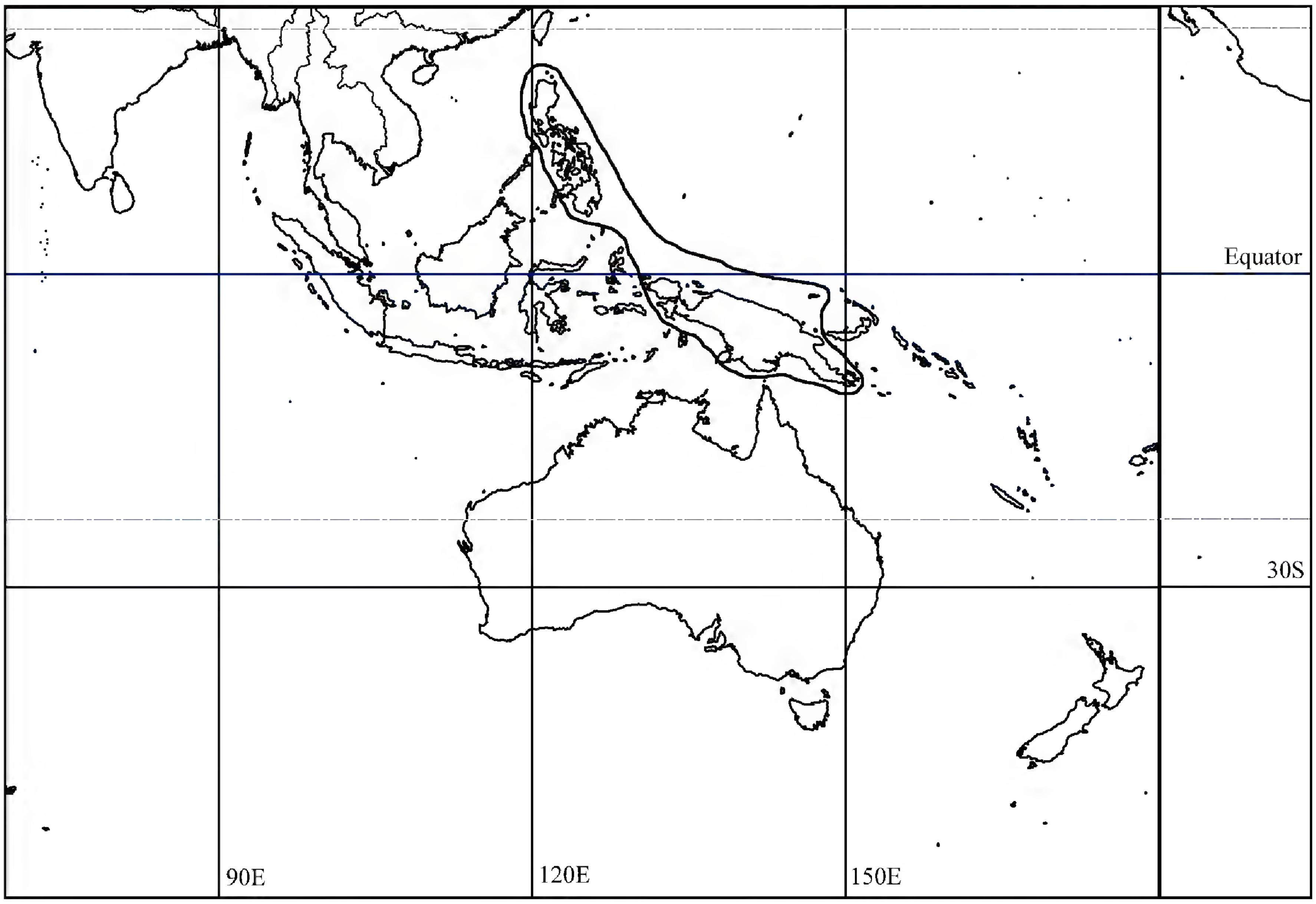

Fig. 9. Distribution map for *Stenochlaena areolaris* (Harr.) Copel.

Chromosomes: $2n$ = c. 73 (fide note on specimen L440260; collector: *Price 578*, Luzon, Philippines).

Distribution and habitat: occurs in the Philippines (from Luzon to Mindanao) and in Papua New Guinea. There are no confimed records from outside Malesia and Papuasia. Fig. 9. This is a tropical species extending from sea level to lower montane areas up to at least 1500 m. From field notes on herbarium specimens *S. areolaris* is an aquatic species, usually an epiphyte and more rarely an epilithic species growing over wet rocks adjacent to a nearby water supply or in stagnant pools. Most specimens examined have been noted as being collected from water pockets in the crowns and leaf bases of *Pandanus* spp. as well as the crowns of various genera of palms and there is nothing to indicate the rhizomes connect to the ground. Some records indicate that *S. areolaris* survives on palms in more open habitats, probably in secondary vegetation. Frequently overlooked by collectors, possibly because it is inconspicuous in the crowns of tall trees.

Notes: 1. Harrington (1877) originally regarded this taxon as a species of *Lomaria,* incorrectly interpreting the presence of a narrow marginal thickening as an indusium which he stated 'is readily overlooked, except in young plants'

2. Collectors have reported that the natural 'tanks' in which this taxon grows are often packed with a tangled mass of rhizomes and roots of *S. areolaris,* sometimes with branches of the rhizomes extending to many water-filled axillary pockets.

Selected specimens examined: PHILIPPINES: Luzon: Laguna, between Cavinte and Luisiana. In water pockets of leaf-bases of *Pandanus simplex*, voucher for 2n = c. 73, *Price 578* (L, NSW, BM, GE, K, MEL, PUH, TAI, U, US); Laguna, between Luisiana and Lucban, *Price 285* (L, NSW, K, MEL, OSAK, PNH, US; Tayabas Prov. Lucban, *Elmer 7961* (L). **INDONESIA:** West New Guinea: Jayapura: Idenburg River, 850m, wedged between leaves of tall *Pandanus, Brass 13417* (A, L); Rouffaer River, 175 m, *van Leeuwen 9909* (B, L); "nova Guinea neerlandica meridionalis", *Versteeg 1102* (L, BO). **PAPUA NEW GUINEA:** West Sepik: Meinet floodplain, N. slopes Bewani Mts, *Croft 1709* (CANB, K, L, NSW); Star Mountains, Busilmin northern foothills 1500m, rhizome entwined in crown of *Pandanus, Croft LAE65705* (L, K, BM). Manus: Manus I., fronds reported to be eaten by villagers, *Croft 1110* (NSW); Morobe: E. of Mongi River, Huon Penin. 700m ridge forest, *Croft 453* (L); Wagau, Numeng Sub-District, epiphytic on *Pandanus* in grassland habitat, 4000 ft (1200m), *Streimann & Kairo NGF35819* (L, LAE); Papuan Islands: Sudest I., Mt Riu, *Croft 774* (NSW).

African and African Island Taxa

5. *Stenochlaena tenuifolia* (Desv.) Moore, Gard. Chron. 1856: 193 (1856).

Basionym: *Lomaria tenuifolia* Desv., Mag. Ges. Naturf. Fr. Berlin Mag. 5: 326 (1811); Synonyms: *Lomariobotrys tenuifolia* (Desv.) Fée, Mém. Fam. Foug. 5: 46 (1852); *Polybotrya tenuifolia* (Desv.) Kuhn, Fil. Afr. 52 (1868); *Acrostichum tenuifolium* (Desv.) Bak. Syn. Fil. 412 (1868); *Lomariopsis tenuifolia* (Desv.) Christ, Farnkr. 42 (1897).

Type: Madagascar, *Commerson* (holo: P n.v.; see Schelpe & Anthony 1986).

Lomaria meyeriana Kunze, Linnaea 10: 509 (1836); *Stenochlaena meyerana* (Kunze) C.Presl, Epim. Bot.166 (1851); *Polybotrya meyeriana* (Kunze) Mett. Fil. Bot. Lips.24, t.1 figs 4 & 7 (1856); *Acrostichum meyeranum* (Kunze) Hook.Gdn Ferns, t.16 (1862); Sp. Fil. 5: 249 (1864). **Type:** South Africa: "In palude sylvatica inter a Omtendo et Omsamculo, 70 m.", *Drège s.n.*, Mar 1832 (lecto: B, isolecto BM, n.v.; designated by Roux 1986: 357).

Literature: Tardieu-Blot, Fl. Madag. Fam. 5, 1: 110, f. 16, 1-3 (1958); Morton, Amer. Fern J. 51: 165 (1965); Schelpe, Fl. Zamb. Pterid. 240, t. 69 (1970); Holttum, Amer. Fern J. 61: 120 (1971); Jacobs, Ferns of Southern Afr. 471, t. 22, 353 (1983); Schelpe & Antony, Fl. Southern Afr., Pterid. 277-8 f.96 (1986); Roux, Pterid. 211 (2008).

Published illustrations: Hooker, (1862) Garden Ferns, pl 16 as *Acrostichum meyerianum*; Jacobsen (1983) f. 353a, b; Burrows (1990) pl. 56.3, illust.82 p.337; Schelpe (1970) t. 69, figs 1, 2. For spores see Tryon & Lugardon 1990 figs 211.4 & 5; Tardieu-Blot, Fl. Madagascar et des Camores (1960) Pl.16, fig. 1, 2, 3 (drawings sterile pinna, fertile frond and spore).

Etymology: in reference to the relatively slender sterile pinnae and to the very slender fertile pinnae and pinnules.

Rhizome extensive, usually at least 20 m long, weakly dorsiventral, but radially symmetrical in cross section, creeping and climbing (and always connected to the ground), 1–2 cm diameter, green to purple-black in fresh material, scaly in young stages becoming ± glabrous except for a few persistent scales; scales dark-brown, small, linear triangular acuminate, often with minute marginal outgrowths 1–5 mm long; *sterile fronds* large, up to 3 m long; *stipes* stramineous, glabrous, reported to be up to 2 cm diameter towards the base and up to about one third the length of the frond; *sterile lamina*, ovate to oblong, 0.5–2 m long and 2–70 (– 75) cm wide, chartaceous to coriaceous. *Sterile pinnae* about 20 pairs, oblong-ovate to linear-lanceolate, tending to be cuneate at the rhachis, 15–35 cm long x 2–3.8 cm wide near the base; pinnae glabrous on both surfaces, glossy green adaxially, dull green abaxially and sometimes with a conspicuous gland at the base on the anterior margin; *margins* finely serrulate to serrate, usually tapering evenly to an acuminate apex which is sometimes shortly attenuate; base of pinna rounded to shortly (and sometimes unequally) cuneate, shortly stalked, not articulate; *terminal pinna* about the same dimensions as the sub-terminal lateral pinnae, occasionally very much longer. *Fertile lamina* bipinnate, occasionally pinnate distally, usually shorter than sterile lamina, typically 0.5–1.5 m long; *fertile pinnae* 25–30 pairs, 8–25 cm or more long and very slender, 1.5–3 mm wide, alternate and sometimes decurrent, adnate to shortly stalked with the gland on the stalk. Fig. 10.

Spores pale yellow-brown to almost colourless, with the tubercles mostly on the irregular ridges, sometimes somewhat coalescent in parallel bands. Fig. 1e.

Chromosomes $n = 72–74$ (Manton & Sledge 1954).

Distribution and habitat: *Stenochlaena tenuifolia* is a widespread species (Fig. 11) extending in favourable habitats from tropical east Africa south through Mozambique to eastern South Africa, including Zululand, Natal, and Transkei, mainly in coastal forests and with isolated populations in the inland Barberton district of Transvaal at over 500 m and also inland at comparable high elevations in Mozambique, Zululand and Natal. The species is a vigorous liana climbing a wide range of tree species and usually is found in humid areas, often on stream margins in swampy places where soil moisture is present even in dry periods.

This species is also present in Zanzibar and the Seychelles and Grande Comoro Island, and also a number of localities in Madagascar (Christensen 1931, Tardieu-Blot 1958). Lorence (1978) reports that *S. tenuifolia* has been recorded but not recently seen in the wild in Mauritius, probably due to the clearing for agriculture of much of the forested areas. I have not seen any records for this taxon from the other islands of the Mascarenes, i.e., Réunion and Rodrigues.

Selected specimens examined: SOUTH AFRICA: Natal: North Coast, 5 m., *de Joncheere SAC 338* (L). **MOZAMBIQUE:** E. of Haroni/Lusitu River confluence, 700 m Manica E. Sofala, *Goldsmith 36/72* (L, SRGH).

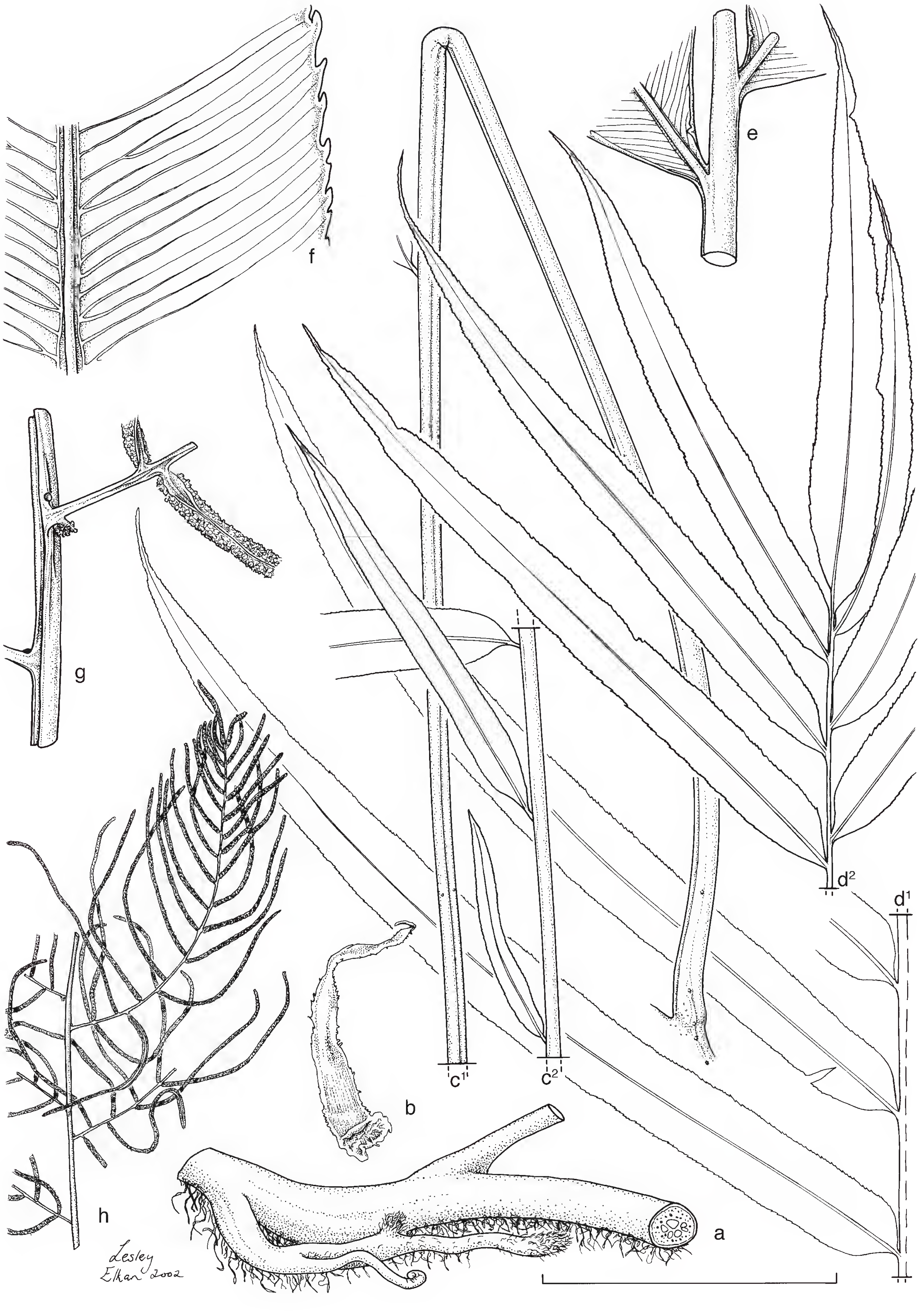

Fig. 10. *Stenochlaena tenuifolia* (Desv.) Moore. **a,** rhizome showing scale covered branch apices and numerous roots and the main rhizome in cross-section; **b,** scale from apical region of the rhizome; **c, d** sterile frond showing full length of stipe (c1), lamina with basal pinnae (c2), pinnae of mid-region (d1) and terminal pinna and several sub-terminal pairs of pinnae (d2); **e,** sterile pinna-base showing the inconspicuous gland; **f,** mid region of sterile pinna showing lateral veins arising from areolar veins closely parallel to the costa; **g,** detail of fertile pinnae and rhachis, adaxial view; **h,** portion of fertile frond showing bipinnate habit, abaxial view. Scale bar: a & h = 10 cm; b = 0.4 cm; c, d = 10 cm; e = 2 cm; f = 1 cm; g = 2 cm. Specimens: a, b, *de Jonchere SAc.338* (L); c–f, *B. Goldsmith 36/72* (NSW); g, h, *J.C. Scheepers 2401* (NSW).

Notes: 1. Schelpe & Antony (1986) reported that the species only produces fertile fronds in areas of high light intensity; plants in closed forests only produce fertile fronds at canopy level.

2. Morton (1965) reported a variant in cultivation in the University California Botanical Garden, introduced from Zululand, South Africa, with extremely narrow pinnae. I have not seen any specimens of this form.

6. *Stenochlaena mildbraedii* Brause, in Brause & Hieron., Bot. Jahrb. Engler 53: 384 (1915).

Type: Fernando Poo, Central Africa: Bioco; Musola oberhalb San Carlos, 500 m (Westkűste), growing on the trunks of the palm, *Raphia*, *G.W.J. Milbraed 6995* (lecto [fide Tardieu-Blot 1964: 354] B20 0121855, photo). Residual syntypes: Cameroon: Südkameruner Waldgebiet: Bezirk Ebolowa, *Mildbraed 5554* (4 sheets, B); Cameroon: Molundu, 21 km Nördlich Molundo *Mildbraed 4192* (3 sheets, B).

Literature: Tardieu-Blot, Mém. L'Inst. Francais D'Afrique Noire 28: 86, 87 pl. 39 f. 5, 6 (p.198) (1953); Tardieu-Blot, Fl. Cameroun 3: 353–354, pl. 34, f.5, 6 (1964); Alston, Fl. W. Trop. Afr. ed. 2, Suppl. Pterid. p. 50 (1959); Holttum, Amer. Fern J. 61: 121 (1971); see discussion below and Schelpe, Conspectus Florae Angolensis, Pteridophyta, 185 (1977); Benl, Acta Bot. Barcinonesia 38: 63 (1967).

Etymology: honouring the German botanist and collector G.W.J. Mildbraed who made several expeditions to tropical West Africa and obtained the Type of this species.

Rhizomes indeterminate, very long, 1.5 cm or more in diameter, frequently branching, scrambling and climbing, adhering to supporting vegetation by means of clusters of short roots and giving rise to successsive spaced fronds, internally with 10 large central bundles in a ring surrounded by 2 rings of more numerous small bundles (approx 30 in each ring); the young growing apex densely clothed with scales; *scales* mid to dark-brown, concolorous, shiny, acuminate and entire or almost so, 6 mm long, 1–1.5 mm wide at base, mostly deciduous, sometimes minutely toothed, weakly bicolorous with a darker mid region and tending to be closely appressed and peltately attached from a raised darker area towards the base; when shed the older more persistent scales leave a small dark raised area on an otherwise glabrous rhizome surface; *sterile fronds* up to at least 3 m in length; *stipes* robust, up to 2 cm diameter at the base tapering to 1 cm diameter and to at least 1.5 m long, glabrous, deeply channelled on the adaxial surface, olive green in fresh material but stramineous to red-brown in dried specimens; *sterile lamina* with 15–50 pairs of pinnae, broad, oblong-lanceolate up to 2 m long, chartaceous to very coriaceous, glabrous. *Pinnae* up to 40 cm long, to 4 cm wide, apices attenuate; basal pairs more spaced, shortly stalked and abruptly shortened, towards the lamina base; pinnae decreasing in length with apical pairs sessile and more crowded, sometimes forming decurrent wings at the rhachis; lamina golden in dried specimens, margins thickened and irregularly sharply serrate to dentate, coriaceous; pinna base entire, rounded to cuneate, not articulate, with a gland near the base on the anterior margin; lateral veins very fine and close together, merging and terminating in the thickened margin; *terminal pinna* similar in dimensions to the lateral pinnae but lacking the gland. *Fertile frond* bipinnate but with same dimensions as sterile frond, the 15–25 (–50) pairs of pinnae the same length or shorter than the sterile and only 4–5 mm wide, widely spaced on the rhachis, subsessile or sometimes distinctly but shortly stalked; *sori* covering almost the whole abaxial surface. Fig. 12.

Spores verrucate, and pale, the tubercles are in several rows and some tubercles appear to coalesce. Fig. 1f.

Distribution and Habitat: native to Tropical West Africa, (possibly the Cameroons), Equatorial Guinea and the island of Fernando Póo (Benl 1988), south to Angola and east including Zaire (Belgian Congo) extending in rainforest habitats along the Congo River and some tributaries to Uganda in tropical east Africa, and usually reported in forest at low elevation, frequently as a climber on *Raphia* palms in swampy areas and along rivers and streams. Fig. 11.

Notes: 1. In the *Flore du Cameroun*, Tardieu-Blot (1964) cites one of the 3 syntypes as 'Type'; effectively lectotypifying the species (ICBN, Art. 9.8). In this work, she illustrates a plant (pl. 34, f.5, 6) with finely and regularly serrate sterile pinnae margins; this figure was taken from an earlier paper (Tardieu-Blot 1953) and does not match the lectotype of *S. mildbraedii* at B. This plant is possibly an undescribed species and is referred to below as sp. 'Cameroon'.

2. This species appears to be a scrambler and climber on a wide range of tree species. The holotype was reported as climbing on a *Raphia* palm and the species has also been recorded on other palms.

3. The external morphology and ecological preferences of *Stenochlaena mildbraedii* are similar to both *S. palustris* and the African *S. tenuifolia* but it usually has much larger fronds than in either of those species. Together with *S. tenuifolia, S. mildbraedii* lacks the characteristic articulation of the pinnae to the rhachis usually so characteristic of *S. palustris*. *Stenochlaena mildbraedii,* from the limited material available, appears to be a much more robust plant, and has a once pinnate fertile lamina clearly differentiating it from *S. tenuifolia*.

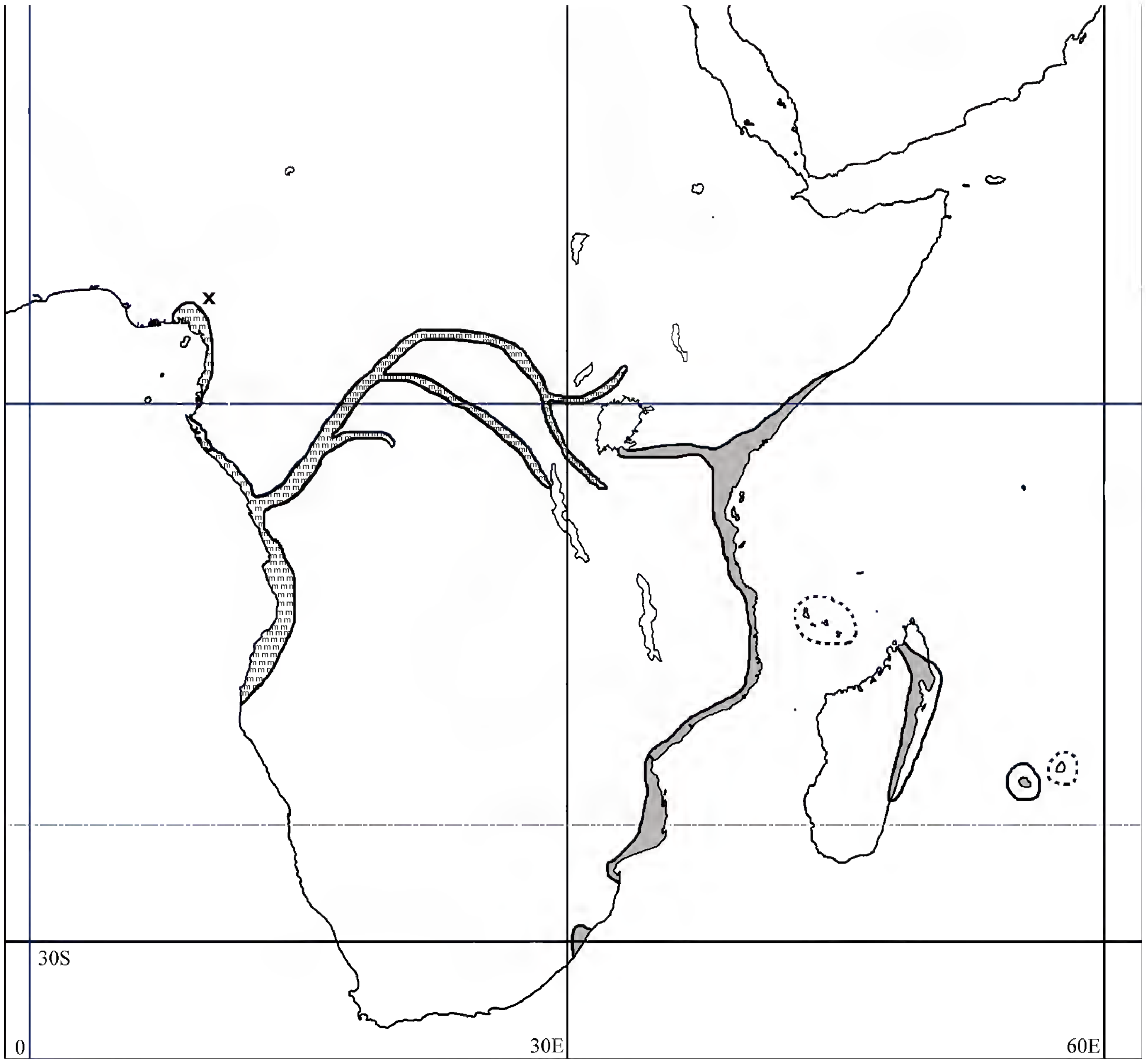

Fig. 11. Distribution map for *Stenochlaena tenuifolia* (Desv.) Moore (grey shading), *Stenochlaena mildbraedii* Brause (mmm) and *Stenochlaena* sp. 'Cameroon' (x).

Specimens examined: ANGOLA: Portuguese Maiomhe: Chiluango *Gossweiler 7953*, 1919, 3 sheets (K) Sheet 1 towards base sterile frond; sheet 2 mid-region sterile frond; sheet 3 several pieces of branching rhizome adhering to tree bark. **UGANDA:** Buddu county, District Masaka U4, 1km N. of Bukeri, 0° 26, 31° 46 E, 1140 m, *Lye* &. *Mani 3494,*12 Jul1969, *ex* Herb Makerere Univ.College (K, 2 sheets). **CAMEROON:** Mpoundou–Seglendom, *Letouzey 3028* (B, photo).

7. *Stenochlaena* sp. 'Cameroon'.

Stenochlaena mildbraedii sensu Tardieu-Blot, Fl. Cameroun (1964: 353–4), Les Pteridophytes de L'Afrique Intertropicale Francaise (1953: 86–87, pl. xxxix, pl. xxxiv).

A specimen at K (*Brunt 323*) from north-west Cameroon is described as a "creeper on tree to 60 ft [over 18 m]". This specimen has fronds that are chartaceous rather than coriaceous; all the sterile pinnae relatively slender, lanceolate, (all under 2 cm wide and up to 16cm long, apices attenuate, shortly stalked at the very slender rhachis, none are articulate and their margins are more regularly and finely dentate. This *Brunt* specimen appears to match the drawing labelled '*Stenochlaena mildbraedii*' in Tardieu-Blot (1964); the illustration of a sterile pinna shows a finely serrate margin and could be either from a sterile specimen of *S. tenuifolia* or possibly from the as yet undescribed taxon. In contrast, the limited material accepted as *S. mildbraedii* and examined in the present study has distinctly coriaceous sterile pinnae with the margins conspicuously sharply and irregularly dentately toothed. Further collections accompanied by careful field observations may indicate that the plant illustrated in Tardieu-Blot and the plant collected by Brunt (both from Cameroon) represent an undescribed taxon.

Specimen examined: CAMEROON: Indop [Ndop] Plain, 3800 ft [c. 1158 m], 5° 45' N, 10° 15' E (Ndop Plain is over 200 km NE of Mt Cameroon at 6°N 10° 35' E), *Brunt 323* (K).

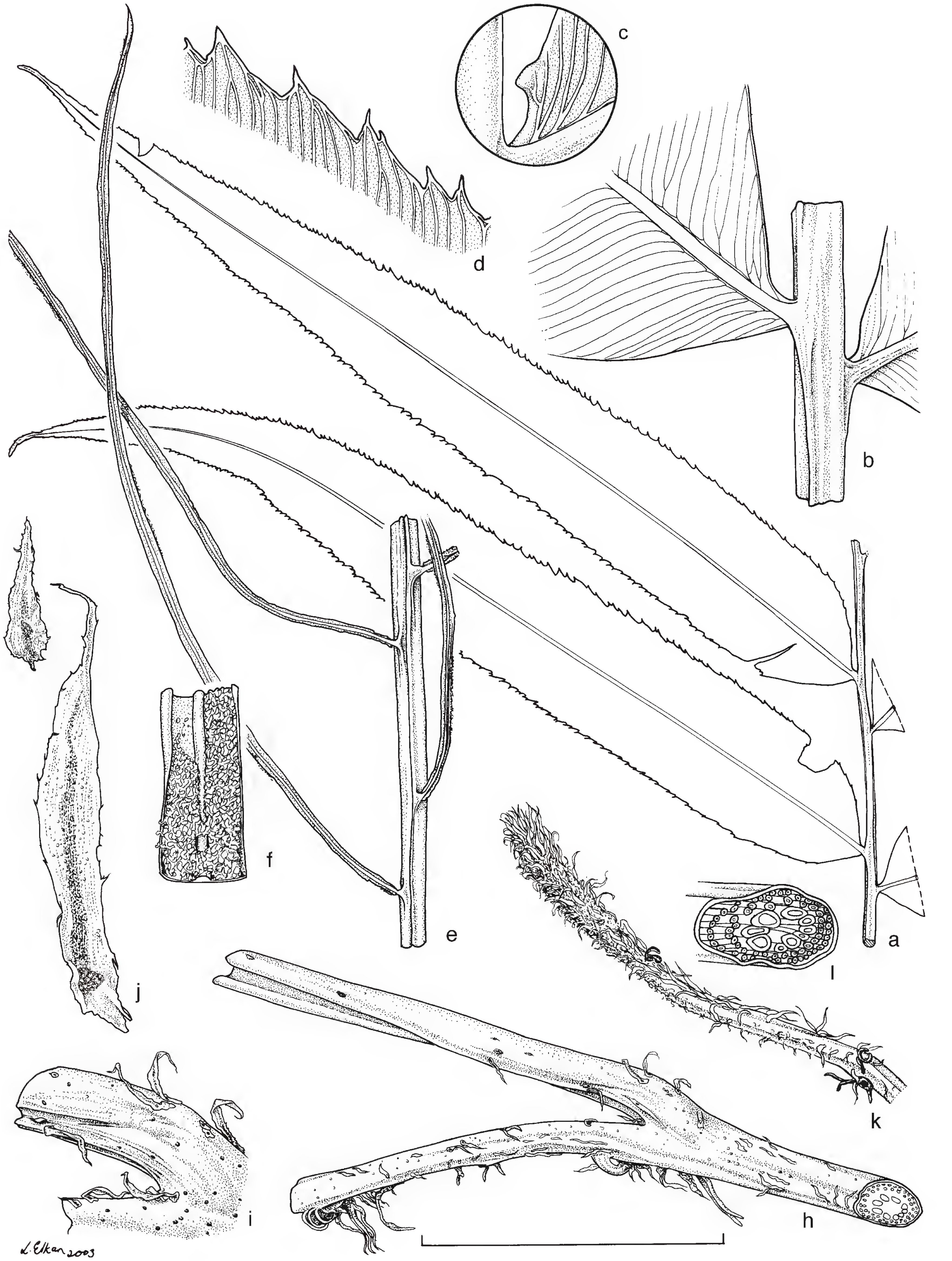

Fig. 12. *Stenochlaena mildbraedii* Brause. **a,** sterile pinnae; **b,** sterile pinnae attachment to rhachis and lateral veins arising from areolar vein close to costa, abaxial view; **c,** gland on sterile pinna; **d,** irregularly dentate margin detail, sterile pinna; **e,** fertile pinnae and rhachis abaxial view; **f,** abaxial detail of fertile pinna; **g,** apical region of rhizome with covering of scales; **h,** rhizome and roots including cross-section and base of stipe; **i,** detail of surface at base of stipe **j,** scales from young rhizome; **k,** young rhizome apex; **l,** rhizome cross section. Scale bar: a, e = 8 cm; b = 2 cm; c, f = 1 cm; d = 1.5 cm; g, h, k = 6 cm; i = 3 cm; j = 0.6 cm; l = 3 cm. Specimens: a–d, *J. Gossweiler 7953* (K); e, f, *K.A. Lye & K.V. Mani 3494* (K)

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